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CONTRIBUTIONS TO PALEONTOLOGY

STUDIES OF CENOZOIC VERTEBRATES
OF WESTERN NORTH AMERICA
AND OF FOSSIL PRIMATES

ARTHUR B. DRESCHER

E. L. FURLONG

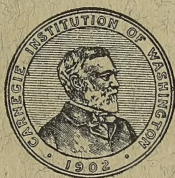
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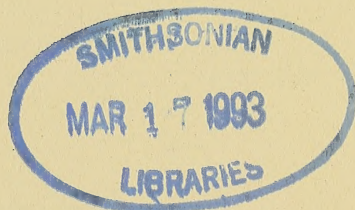
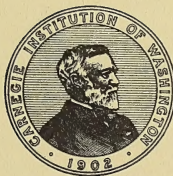
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CONTRIBUTIONS TO PALEONTOLOGY

I

LATER TERTIARY EQUIDAE FROM THE TEJON HILLS,
CALIFORNIA

ARTHUR B. DRESCHER

With three plates and six text figures

[Issued May 1, 1941]

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LATER TERTIARY EQUIDAE FROM THE TEJON HILLS, CALIFORNIA

INTRODUCTION

Fossil vertebrates were first discovered in continental sediments of the Tejon Hills (for location see fig. 1) in 1911, by R. W. Pack, of the U. S. Geological Survey. The occurrence of these fragmentary specimens was briefly described at a meeting of the Pacific Coast Paleontological Society in 1913 (Merriam and Pack, 1913). Thereafter some collecting was done by the University of California party of 1915, the results of which were presented in papers by Merriam (1915*a*, 1915*b*, 1916). During the latter part of 1928, field parties of the California Institute of Technology obtained a much larger fauna than that previously collected in the Tejon Hills. As a result of further field work by R. W. Wilson, R. M. Leard, Jack Dougherty, and the writer in 1938, considerable fossil material was obtained from this area, and the existence of three distinct faunas was disclosed. These were collected at seven localities along the ridge to the south and west of Comanche Creek (see map, fig. 2).



Fig. 1. Index map of a part of southern California, showing location of the Tejon Hills

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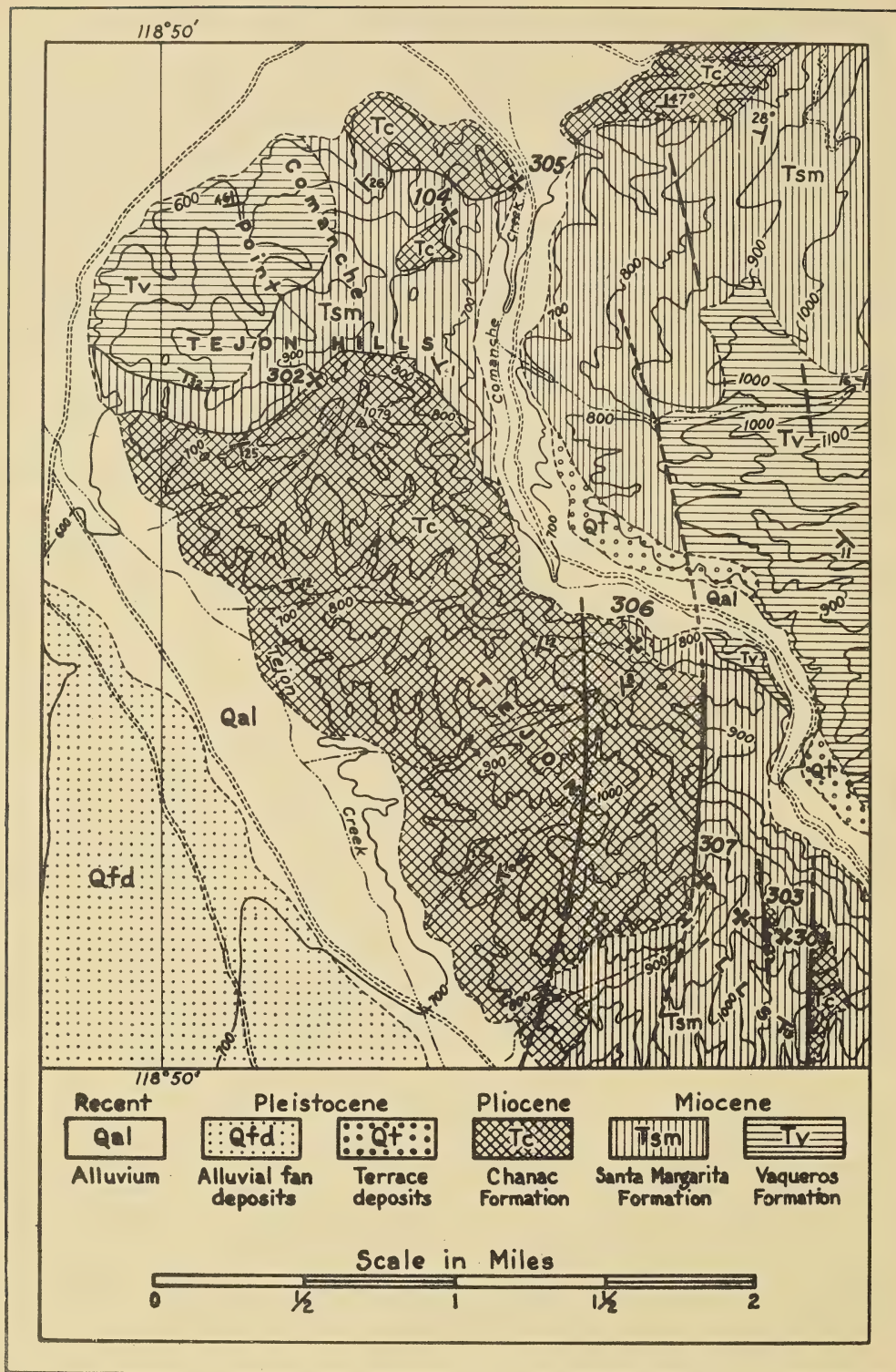


Fig. 2. Geology of a part of the Tejon Hills, slightly modified after H. W. Hoots, U. S. Geol. Surv. Bull. 812. Note position of Calif. Inst. Tech. Vert. Pale. localities.

The present research limits itself to a study of the fossil Equidae of the Tejon Hills, and gives evidence of the presence of two groups of horses, one occurring in the Santa Margarita formation, the other in the Chanac formation. Each group is apparently confined to its respective horizon. Recently Stirton (1939a, 1939b) called attention to the presence of two equid faunas in the Tejon Hills. A preliminary survey of the mammals other than horses reveals the fact that a similar segregation in time is suggested by the relationships of certain forms. Observations of the stratigraphy likewise point to this conclusion, and indicate, furthermore, that the lowest and therefore the earliest of the several fossil sites occurs in a continental phase of the Santa Margarita formation. A comparison of the material previously described from the Tejon Hills with that obtained in recent years leads to the conclusion that the former specimens came from the lower horizon and represented float material. The suggestion that two faunas were present in the first collections made probably followed the recognition of an association of *Merychippus* and *Hipparion* (*Nannippus*). The type of horse originally described as *Merychippus*, however, is actually *Pliohippus tehonensis*.

ACKNOWLEDGMENTS

I wish to express my appreciation of the assistance rendered by Dr. Chester Stock in the course of the present study. Dr. R. W. Wilson offered many helpful suggestions. I am indebted to the U. S. National Museum, the Nebraska State Museum, and the Museum of Paleontology, University of California, for the loan of comparative material. The illustrations were prepared by David P. Willoughby and John L. Ridgway.

OCCURRENCE OF MATERIAL

All fossil specimens collected by the California Institute of Technology occurred within a zone approximately 150 feet thick which included the uppermost 50 feet of the Santa Margarita formation, the "transition zone," and approximately 50 feet of the typical buff sediments of the Chanac formation. The fossil vertebrates are not evenly distributed within this zone, but are definitely confined to three subzones. The lowest or oldest of these is represented by three quarries, C.I.T. Vert. Pale. localities 303, 304, and 307, all of which are located in the Santa Margarita formation as mapped in this area by H. W. Hoots (1930). Above this horizon is another subzone, located near the Santa Margarita-Chanac contact and regarded as a "transition zone," in which three quarries, C.I.T. localities 104, 302, and 305, were developed. The latter three sites are on the nose of the anticline in the northwestern part of the area. The highest subzone is situated geographically midway between the two zones already mentioned, and in this horizon occurs C.I.T. locality 306. The fauna from

306 is meager, and includes a number of small carnivores and a large *Hipparton*, probably the species *H. cf. mohavense*. In the present paper little further mention is made of this highest horizon, and the two older subzones will be distinguished as the lower and upper Tejon Hills faunas. The upper Tejon Hills fauna and that from locality 306 contain types hitherto not described from the Tejon Hills. All the quarries are in sandy clays interbedded with coarse gritty sandstones.

PRESERVATION OF MATERIAL

The fossil material is well preserved, especially in the lower zone. Unfortunately, no complete skulls or lower jaws were obtained. Several complete series of cheek teeth are available. The bones and teeth do not show evidence of water wear or long exposure to weathering. Lack of complete specimens may be due to breakage incurred before burial, as, for example, in and about a water hole where disturbance and destruction of material resulted from the presence of carnivores and ungulates.

The conditions of deposition were probably those of a flood plain close to the shores of the Santa Margarita sea. It is worthy of note that the deposits show cross-bedding of a fluvial type. Also of significance perhaps is the presence of several carapaces of tortoises associated with the mammalian bones. Vertebrate materials found with marine invertebrates in the Santa Margarita formation may have been eroded and redeposited after accumulation in continental beds or may have been laid down on a sea beach.

STRATIGRAPHIC RELATIONSHIPS OF FAUNAS

The Santa Margarita formation in the Tejon Hills varies in thickness from 100 to 1000 feet (Hoots, 1930). The upper part of this formation consists of dominantly grayish-white marine sediments in the northwestern part of the Comanche Point area and its stratigraphic equivalent, the greenish nonmarine gravels to the southeast. In the near vicinity of locality 303, white marine beds with a typical Santa Margarita invertebrate fauna underlie the Chanac formation with apparent conformity (Buwalda, 1916), the marine fossils occurring only 25 feet stratigraphically below the vertebrate-bearing horizon. A short distance to the west, imperfectly preserved invertebrate fossils were found above fragmentary teeth and bones of *Pliohippus tehonensis*, definitely placing this form in the Santa Margarita formation.

Unless reworking of the marine deposits and invertebrates has taken place, no marine Santa Margarita was deposited in the southeastern part of the area to the north of Tejon Creek. Marine deposits lower in the Santa Margarita formation may exist here, but no invertebrate-bearing beds were seen, and the lithology is that of typical fanglomerates, in contrast with the chalky-white to grayish marine sands.

Hoots states that "the light gray Santa Margarita beds grade upward into the overlying buff strata through a transition zone 50 to 100 feet thick that is composed of beds of alternating gray and buff color" (Hoots, 1930). The contact recognized in the present paper is at the base of the lowermost buff-colored bed; in other words, the "transition zone" is included in the Chanac formation.

It is rather unusual that the striking differences which distinguish the two principal faunas of the Tejon Hills should be associated with a stratigraphic separation of merely 50 feet, involving strata which evidently were deposited rapidly, as is indicated by the coarse grain and shape of particles of the sediments and by the cross-bedding. Evidence of the small time interval between the two faunas may be seen best in the small down-faulted block of sediments in which quarry 304 is located. This is one of the few places in the Tejon Hills where the exposed section is of such thickness as to include both horizons. Less than 50 feet above the level of this quarry the Chanac-Santa Margarita contact is exposed, and fossil rodents like those collected at quarry 302, a contact quarry, were found in similar sediments. Approximately 50 feet above this contact, in the same fault block, occur fragmentary limb bones of a large horse and camel. This horizon is tentatively assigned to the third (uppermost) subzone because of the similarity of the sediments and on the basis of the stratigraphic position.

Although no definite field evidence was obtained of an important break in deposition between the Santa Margarita and Chanac formations, such a break is believed to exist at the base of the "transition zone." It appears possible that a considerable thickness of coarse sediments was deposited and later removed by erosion without leaving a recognizable disconformity in the sediments. That the difference in faunas is due to a difference in environmental conditions seems unlikely in view of the proximity of the faunas and in view also of their stage of development.

Thus, the history of this portion of the Tejon Hills, as interpreted from the stratigraphy and occurrence of fossil materials, may be summarized as follows: With the coming of upper Santa Margarita time, environmental conditions changed from marine to nonmarine as the shore line of the sea retreated to the northwest, furnishing an opportunity for preservation of a record of the mammalian life, probably on a wide flood plain near the sea. At the time when the earliest mammalian assemblage was being deposited in the southeastern portion of the Tejon Hills, the northwestern area was still under marine waters, although a probable oscillation of the shore line permitted an interdigitation of continental beds containing vertebrate fossils with invertebrate-bearing marine deposits. These conditions continued into Lower Pliocene time, when renewed elevation initiated a period of erosion which removed some of the sediments previously deposited. Following this

episode, there occurred a period of oscillation in the conditions of deposition, during which the "transition zone" of alternating gray and buff sediments, namely the lower Chanac, was laid down. Finally, the typical continental buff fanglomerates of the upper Chanac formation were deposited.

AGE AND CORRELATION

The lower fauna of the Tejon Hills is associated with, and probably essentially equivalent in time to, a marine invertebrate assemblage of Santa Margarita age. U. S. Grant IV is of the opinion¹ that the invertebrate fauna of the Tejon Hills cannot belong to the Lower Pliocene as we understand the invertebrate faunal characteristics of that epoch in California. He notes, furthermore, that if the species in this assemblage have been correctly identified, the fauna is pre-Jacalitos in age. Since the Jacalitos is generally considered to be Lower Pliocene, this places the Santa Margarita formation in the Miocene. Recently some workers (Gester and Galloway, 1933) have considered the Jacalitos to be part of the Middle Pliocene Etchegoin formation, and if this is correct, the allocation of the lower Tejon Hills fauna to the Lower Pliocene (Stirton, 1939a, 1939b) is a logical conclusion. The present study, however, shows that the lower fauna from the Tejon Hills is more primitive than the Orindan, which Stirton places at the base of the Pliocene column. Hence, taking into account the likelihood of an unconformity between the formations at Comanche Point, and the existence of a Miocene invertebrate fauna above the vertebrates of the lower horizon, the view that the latter are Upper Miocene in age seems justified. Thus, there would appear to be no important discrepancy in the time scales based on terrestrial vertebrates and marine invertebrates.

That the faunas discussed here are not younger than Lower Pliocene is shown by the stages of evolution exhibited by members of the Equidae. Presence of *Hipparion molle* might indeed be taken as an indication of later time, but the reported occurrence of this form is not substantiated by our present knowledge. *Merychippus* sp. was also reported in the first collection from Tejon Hills, but better material has shown this type to be *Pliothippus tehonensis*. The forms from the lower quarries show a number of primitive characteristics as compared with Lower Pliocene types, and the lower fauna is probably the youngest Miocene assemblage known from the Pacific Coast region.

The vertebrate-bearing beds of the Kern River region are considered to be younger than the Chanac beds of the Tejon Hills. The hipparion species in the Kern River fauna is clearly a more advanced form than the species recognized in the Tejon Hills area. A *Pliothippus* which occurs in the Kern River is hardly distinguishable from *Pliothippus leardi*, n. sp., of the Tejon Hills, although in some characters it exhibits a more advanced stage of evolution

¹Personal communication.

than the latter. It seems probable that the Kern River species was derived from *P. leardi*.

The presence of *Hipparion molle* in the Jacalitos at several localities on the west side of the San Joaquin Valley (Merriam, 1915b) similarly suggests that the strata containing this type are of later age than the horizons in the Tejon Hills. Arnold and Anderson as well as Nomland mention the occurrence of *Pliohippus* sp. in the basal Jacalitos of the Coalinga region and point out that it is similar to *Pliohippus tehonensis* (Arnold and Anderson, 1910; Nomland, 1916). The Jacalitos form, however, is probably more advanced than the latter.

Nannippus tehonensis occurs in the Neroly and Orinda of the San Francisco Bay region (Stirton, 1939a, 1939b). A similar form was reported some years ago from the eastern flank of the Diablo Range southwest of Modesto (Merriam, 1916) and more recently from several scattered localities in the same region (Stirton, 1939b). Again, *N. tehonensis* has been reported from the Mint Canyon formation (Maxson, 1930; Stirton, 1933). These occurrences suggest that the faunas are more or less equivalent to that of the lower zone at Comanche Point (Stirton, 1936, 1939). The Mint Canyon, however, on the evidence of stratigraphy (Jahns, 1939), is probably Miocene, although later than the Barstow. Moreover, the *Nannippus* species from both southern localities are more primitive than those of the San Francisco Bay area. It would appear then that there are at least two occurrences of hipparions in the Upper Miocene of this region. Similar occurrences may be expected in the Ellensburg and possibly in the Neroly.

Present evidence tends to show that the upper Tejon Hills fauna is slightly more advanced than the Siesta. Teeth referred to *Hipparion* cf. *mohavense* from the Chanac, for example, are slightly higher-crowned than those of a comparable form from the northern locality. This conclusion was also reached by Stirton (1939b).

Lower teeth of *Hipparion condoni* from the Ellensburg formation of Washington (Merriam, 1915b) are very similar to those of *Nannippus tehonensis*, and indicate apparently a close relationship in time. A fauna, as yet not completely described, from the Smith Valley beds of Nevada contains a *Pliohippus* similar to *P. leardi* and a species of *Hipparion* which is smaller than *Nannippus tehonensis* and in which the upper teeth have more complicated fossettes. A single upper tooth of *Pliohippus* from near Sunland, California, reported to have come from the Saugus formation, is similar to those of the large *Pliohippus* from the Tejon Hills.

Neohipparion gratum of the Great Plains Tertiary is more advanced than *Nannippus tehonensis*. This is indicated by its more hypsodont teeth, greater elongation of protocone, absence of spur on this cusp, more distinctly curved crown, greater flattening of outer walls of protoconid and hypoconid, and less angular gutter. (See also page 11.)

Two horses from the Ricardo formation (Merriam, 1919) appear to be slightly more advanced than those of the Chanac, although the Ricardo formation may be in part equivalent to the upper Chanac. *Hipparion* sp. B from the Ricardo is similar to *Nannippus* cf. *tehonensis* of the upper fauna. The Barstow forms are distinctly less advanced than those from the lower horizon of the Tejon Hills.

Hipparion near *mohavense*, from the Puente formation (Stock, 1928), appears to be almost identical with the species *H.* cf. *mohavense* in the Tejon Hills upper fauna. This suggests that the Puente formation is in part Lower Pliocene.

CORRELATION CHART OF VERTEBRATE FAUNAL HORIZONS

Age	Pacific Coast province	Great Basin province
Middle Pliocene	Etchegoin Pinole Kern River Jacalitos	Thousand Creek Rattlesnake
Lower Pliocene	Upper Tejon Hills (Chanac) Siesta Orinda	Upper Ricardo Lower Ricardo Avawatz*
Upper Miocene	Mint Canyon Lower Tejon Hills (Santa Margarita)	Barstow

* Henshaw, 1939.

DESCRIPTION OF SPECIES

EQUIDAE FROM THE SANTA MARGARITA FORMATION

Nannippus tehonensis (Merriam)

Neohipparion gratum tehonense, n. subsp. Merriam. J. C. Merriam, Mammalian remains from the Chanac formation of the Tejon Hills, California. Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, no. 8, pp. 118-120, figs. 1-9, 1916.

Hipparion gratum tehonense Merriam. H. F. Osborn, Equidae of the Oligocene, Miocene and Pliocene of North America, iconographic type revision. Mem. Amer. Mus. Nat. Hist., vol. 2, p. 189, fig. 152, 1918.

Nannippus tehonensis (Merriam). R. A. Stirton, Cenozoic mammal remains from the San Francisco Bay region. Univ. Calif. Publ., Bull. Dept. Geol. Sci., vol. 24, no. 13, pp. 347-352, figs. 10-24, 1939.

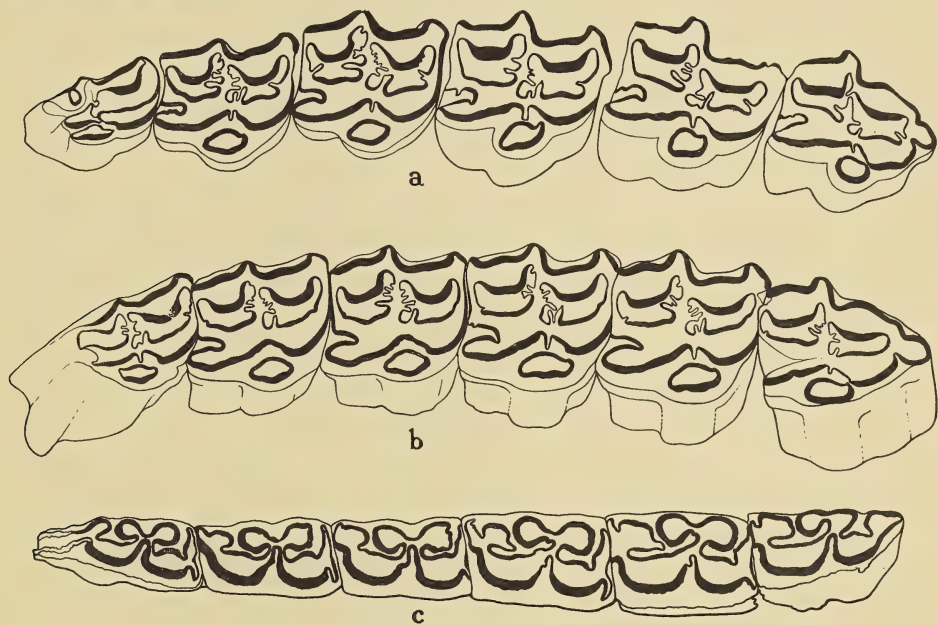


Fig. 3. *Nannippus tehonensis* (Merriam). a, slightly worn P²-M³, no. 2591; b, moderately worn P²-M³, no. 2598; c, moderately worn P₂-M₃, no. 2606. Natural size.

Calif. Inst. Tech. Vert. Pale. locality 303.

This species was originally described as *Neohipparion gratum tehonense* by John C. Merriam in 1916 on the basis of isolated teeth. Certain constant and important differences between the California and Great Plains forms necessitate the recognition of the former as of specific status. These differences have not been adequately established in print, so far as the writer is aware. They may be stated as follows: *Neohipparion gratum* has higher-crowned molar teeth with crowns more curved. Its upper teeth have an isolated enamel lake in the hypocone formed by total constriction of the posthypoconal valley. Moreover, in these teeth the protocone is more elongate, the fossettes are

relatively wider transversely, and the parastyle and mesostyle are weaker than in the California type. In the lower molars *Neohipparion gratum* differs from *Nannippus tehonensis* in having a shallower gutter and more complex plications of the enamel in the central valleys. The valley in the outer wall does not extend so deeply into the interior of the tooth and is often characterized by a plication between metalophid and hypolophid.

In view of these differences and in view also of the larger collection now available at the California Institute of Technology from the Tejon Hills, it seems desirable to record additional characters of *Nannippus tehonensis*.

Upper dentition. The upper cheek teeth are moderately high-crowned and heavily cemented. They are squarish in shape and only slightly curved. The premolars are noticeably larger than the molars in crown size. The protocone is small, and rounded to semilenticular, that of M^2 and M^3 being relatively flat. As a rule, this cusp is not separate at the base in P^2 . In the premolars, and also occasionally in the molars, the protocone has a spur which projects in the direction of the protoconule and with which it becomes united in advanced stages of wear. The protocone is approximately equal to the hypocone in size. The hypocone is given definition by a strongly developed posthypoconal valley. The pli caballin is a simple fold. The outer borders of the fossettes are transversely narrow. One of the plications on the border of the prefossette is almost completely pinched off to form an isolated lake, but it is never completely isolated as in *Neohipparion gratum*. The crown tapers definitely toward the base, so that the tooth size becomes distinctly smaller as wear increases. The mesostyle approximates the parastyle in heaviness, although it is slightly more slender than the latter in the premolars. Frequently the premolars, and sometimes the molars, show a faint metastyle. The protocone is less flattened in the milk teeth than in the permanent grinders. The crown is subhypsodont and is not heavily cemented.

Lower dentition. The lower molars have high crowns and are also heavily cemented. They are rectangular in shape and taper toward their bases. As in the upper teeth, the premolars are much larger than the molars. The metaconid-metastylid column is distinct to the base of the tooth. It is long anteroposteriorly, and has a moderately deep to shallow gutter. The outer walls of protoconid and hypoconid are either slightly flattened or round. A prominent style is present at the anteroexternal corner of the protoconid. An outer valley extends deeply into the tooth. The deciduous lower molars do not have a heavy coating of cement.

Several fragmentary limb elements are in the collection, but the specimens apparently have no characters of diagnostic value.

Measurements of dentition of Nannippus tehonensis (in millimeters)

The transverse diameter of the crown does not include the mesostyle, but is measured from the farthest indentation of the paraconid-metaconid wall to the farthest lingual projection of the protocone (Bode, 1935). This method of measuring makes possible a comparison of a greater number of teeth, since the mesostyle is often broken away. Moreover, it gives a better indication of the general shape of the tooth. The anteroposterior length of the crown in the upper molars is taken between the wearing facets on the anterior and posterior faces of the tooth. In the lower molars the width of the tooth is measured across the enamel walls of the metaconid and protoconid.

A: C.I.T. no. 2591 (fig. 3a)

B: C.I.T. no. 2598 (fig. 3b)

C: C.I.T. no. 2604

D: C.I.T. no. 2606 (fig. 3c)

Anteroposterior diameter				Length of protocone		Length of metaconid-metastylid column	
A	B	C	D	A	B	C	D
P ²22.1	22.4	P ₂19.3	20.4	5.1	6.4	8.6	8.4
P ³19.0	18.9	P ₃18.8	19.1	5.9	7.2	10.4	11.1
P ⁴19.1	18.7	P ₄19.4	18.8	6.3	7.7	10.5	11.1
M ¹18.3	17.8	M ₁18.5	17.9	5.8	6.4	10.8	10.6
M ²16.8	17.4	M ₂18.8	17.8	5.8	6.1	9.7	10.0
M ³15.8	16.4	M ₃18.7	17.5	5.9	6.4	7.4	8.9
Transverse diameter							
P ²14.0	13.3	P ₂ 8.2	8.0				
P ³13.0	14.6	P ₃10.5	10.7				
P ⁴14.6	14.1	P ₄10.1	10.4				
M ¹14.7	14.2	M ₁ 9.2	9.4				
M ²13.2	14.5	M ₂ 8.8	8.9				
M ³ 8.9	10.4	M ₃ 6.8	7.7				

Length of upper molar series: A, 50.9; B, 52.2

Length of upper premolar series: A, 58.2; B, 60.5

Length of lower molar series: C, 56.0; D, 52.9

Length of lower premolar series: C, 57.5; D, 59.0

Maximum length of crown of unworn specimens, 40

In the light of the larger collection available, the teeth from the Tejon Hills originally referred to *Neohipparion* near *molle* by Merriam are now seen to be a variation of the dentition characteristic of *Nannippus tehonensis*. All the differences listed by Merriam can be duplicated in specimens of the latter species. Similarly, those teeth referred to *Neohipparion* near *gratum tehonense* by Merriam are likewise referable to *Nannippus tehonensis*.

Nannippus tehonensis closely resembles the species *Hipparion condoni* as based upon the lower molars described by Merriam from the Ellensburg formation of

Washington (Merriam, 1915b). It differs only in slightly smaller size, but this difference does not appear to be of sufficient importance to separate the two. However, since no upper teeth have thus far been described from the Ellensburg, and since the type specimen of *H. condoni* is now not available for comparison, it seems best to await larger collections from the Ellensburg before a more detailed statement is made concerning the relationships of these species.

The species of *Nannippus* from the lower horizon of the Tejon Hills differs from *Neohipparion molle* and from the hipparion from the Kern River beds in its smaller size and in the shorter and smaller protocone. *Hipparion dolichops* Gidley from South Dakota appears to be very similar, but is larger, with more complicated fossette borders in the cheek teeth. In this species also the fossettes are wider transversely and the protocone is flatter than in *Nannippus tehonensis*.

Although teeth of *N. tehonensis* are similar to those referred to *Nannippus* by Stirton from the vicinity of San Francisco Bay, several differences prevail which suggest that the species from the Tejon Hills is more primitive than the northern forms, and which may ultimately necessitate a recognition of the latter as a separate species. On the other hand, more material from the northern localities may demonstrate that the differences are due to individual variation. *Nannippus tehonensis* from the type locality is slightly less hypsodont, the maximum height of the unworn crown being 40 mm., as compared with 44 mm. in the specimens described by Stirton. There appears to be less tendency for the protocone to be separate from the protoselene in teeth from the Tejon Hills. Many specimens are available in which this cusp is not distinct at 15 or more millimeters above the base of the tooth. Stirton states that in only one specimen among a number of teeth from the Orinda is the protocone connected with the protoselene 8.5 mm. above the base; in all others apparently the protocone is separate to the base (Stirton, 1939b). Associated with this character, and pointing toward relation with *Merychippus*, is the frequent presence of a spur on the buccal side of the protocone, which becomes connected with the protoselene with wear. In specimens of *N. tehonensis* from the type locality the crown is slightly less curved and slightly smaller than that in the teeth described by Stirton. The lower teeth have a prominent protostylid.

Material of a *Nannippus*-like form from the Mint Canyon formation is insufficient to permit a satisfactory comparison with *N. tehonensis*. A single tooth, M^s, described by Maxson and referred by him to the genus *Merychippus*, has an open postfossette, an unusual character which may be duplicated in specimens from the Tejon Hills that are regarded as variants of *N. tehonensis*. However, the tooth has more slender styles and the crown appears to show slightly greater curvature than in specimens of *N. tehonensis*. On the

basis of these characters the Mint Canyon specimen may represent a slightly more primitive type of horse than *N. tehonensis*. It is significant that teeth compared with those of *Hipparion mohavense* occur higher in the Mint Canyon section. That portion of the Mint Canyon formation whence the single tooth comes may be related in time to the lower zone of the Tejon Hills.

Pliohippus tehonensis (Merriam)

Protohippus tehonensis Merriam. J. C. Merriam, Mammalian remains from the Chanac formation of the Tejon Hills, California. Univ. Calif. Publ., Bull. Dept. Geol., vol. 10, no. 8, p. 125, figs. 14, 15, 1916.

This species from the Tejon Hills was described by Merriam on the basis of a single upper molar, no. 21779 in the University of California collections. To this species is assigned also a lower premolar, no. 21484. Although much fossil material has subsequently been found by field parties of the California

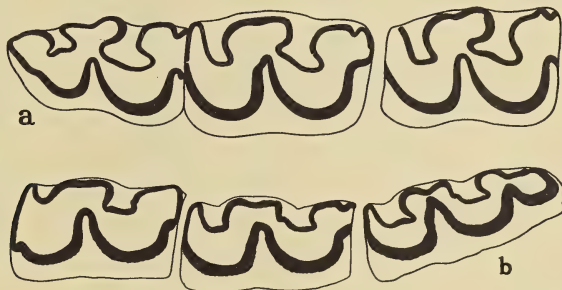


Fig. 4. *Pliohippus tehonensis* (Merriam). *a*, moderately worn P_2 - P_4 , no. 2617; *b*, moderately worn M_1 - M_3 , no. 2618. Natural size.

Calif. Inst. Tech. Vert. Pale. locality 303.

Institute of Technology, no additional complete upper teeth of this species were obtained. A sufficient number of fragments have been uncovered in place, however, to demonstrate that the species belongs to the lower fauna. Moreover, two specimens of the lower dentition, C.I.T. no. 2617 with P_2 to P_4 and no. 2618 with M_1 to M_3 , were obtained from quarries in the Santa Margarita formation.

In 1935 Stock described a section of a lower jaw, C.I.T. no. 1825, containing Dp_2 - Dp_4 and M_1 , taken from a depth of 5217 feet in the core of a well located several miles northwest of Comanche Point (Stock, 1935). This specimen was identified as *Protohippus tehonensis* and the characters of the milk dentition and of M_1 were given.

M_1 in the specimen from the well core is practically unworn, whereas in those teeth obtained at the surface the crowns are worn. The latter demonstrate that with increased wear the gutter between metaconid and metastylid becomes shallower and almost disappears. Similarly, the internal valleys tend to be reduced, especially in the molars. The external valley, however, remains deep although the cant to the front becomes less pronounced. In

general, with advancing wear the appearance of the occlusal surface becomes more like that in *Merychippus*. The posteroexternal style, which in the milk teeth is very prominent, is slightly less so in the permanent teeth. On the other hand, the anteroexternal style practically disappears, although it is still seen in a reduced state in M_1 . The length of the metaconid-metastylid column is less in the permanent dentition than in the milk dentition, and seems to decrease somewhat with wear. The entoconid is large.

Measurements of dentition of Pliohippus tehonensis (in millimeters)

Specimen no.	Anteroposterior diameter	Transverse diameter	Length of metaconid- metastylid column
C.I.T. 2617, P_2	23.9	11.4	8.9
C.I.T. 2617, P_3	24.1	13.7	9.1
C.I.T. 2617, P_4	23.8	13.8	9.7
C.I.T. 2618, M_1	21.9	11.0	8.4
C.I.T. 2618, M_2	22.6	10.3	8.4
C.I.T. 2618, M_3	26.5	9.1	7.9
U.C. 21484, P_4	22.8	11.7	9.2
C.I.T. 1825, M_1	26.3	11.4	11.8
C.I.T. 1825, Dp_3	26.4	14.9	13.9
C.I.T. 1825, Dp_4	28.6	13.8	12.9
U.C. 21779, M^1	22.5	20.5

There are differences between the specimen from the well core and teeth obtained from surface exposures of the Santa Margarita. Particularly is this true of the relative length of the metaconid-metastylid column and of the width of the tooth. Although it is possible that the specimen from the well core represents a species distinct from *P. tehonensis*, it appears more likely that the differences in dimensions are due to individual variation and to stage of wear.

An upper tooth from the Jacalitos of the north Coalinga region, which according to Merriam resembled *P. tehonensis* (Merriam, 1916), appears to be more advanced than this species and is similar to the *Pliohippus* species from the Chanac (upper Tejon Hills fauna) in the peculiar shape of the protocone. A fragmentary upper molar assigned to *Merychippus* sp. by Merriam in his first publication on the fauna from the Tejon Hills resembles *P. tehonensis* in size and in the character of the fossettes.

EQUIDAE FROM THE CHANAC FORMATION

Hipparion cf. *mohavense* Merriam

Hipparion (?) *mohavense* Merriam. J. C. Merriam, New protohippine horses from Tertiary beds on the western border of the Mohave Desert, Univ. Calif. Publ., Bull. Dept. Geol., vol. 7, no. 23, pp. 436-440, figs. 1a-3b, 1913.

The material in the collections of the California Institute of Technology, referable to this type, consists of ten upper and twelve lower cheek teeth, both permanent and deciduous. There are no specimens that can be directly associated.

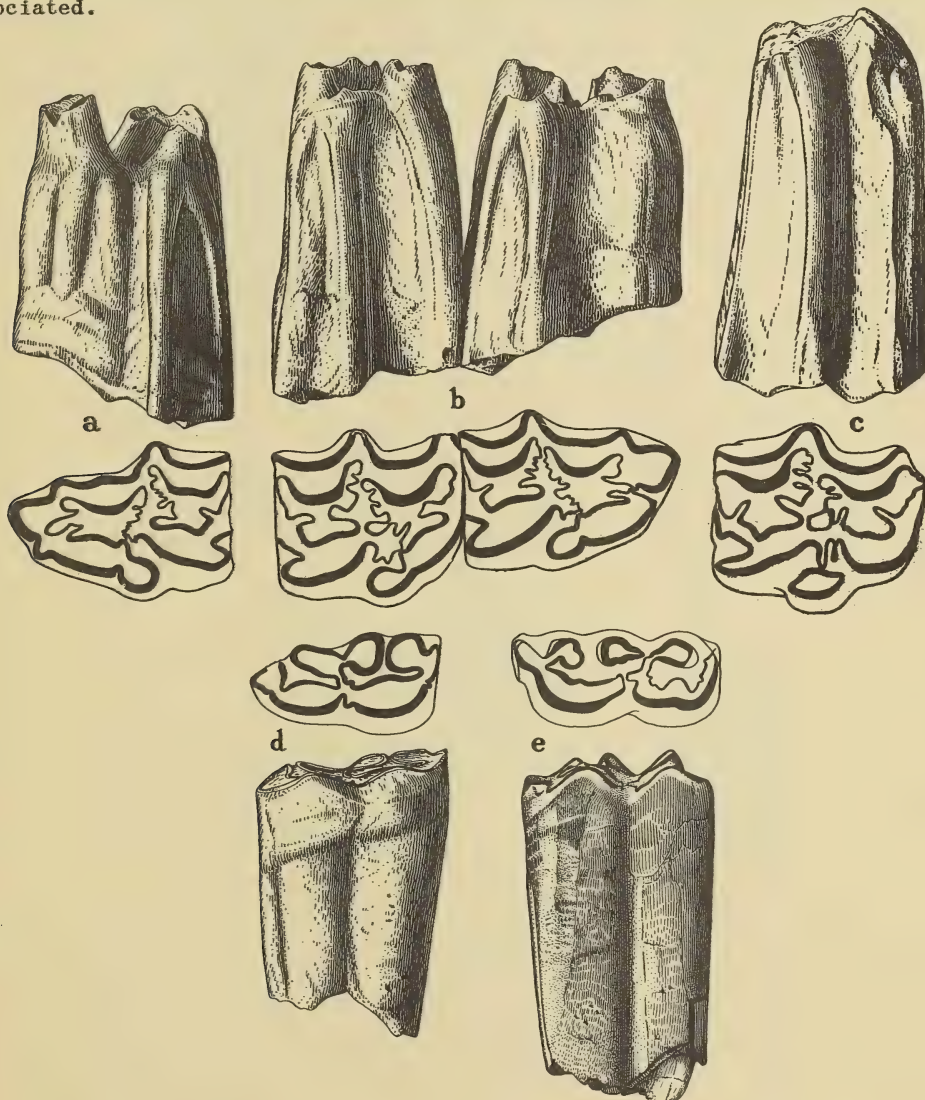


Fig. 5. *Hipparion* cf. *mohavense* Merriam. a, P², no. 1177; b, P² and P³, nos. 1178 and 1179; c, P⁴, no. 1180; d, P², no. 1176; e, M₁, no. 2623. Natural size. Calif. Inst. Tech. Vert. Pale. locality 104.

These specimens differ from the type of *Hipparion mohavense* (Merriam, 1913) in having a smaller protocone which shows less tendency to become discrete; in several teeth the protocone and protoconule are connected in crowns showing only moderate wear. The enamel plications of the fossette borders are slightly less complicated than in the Ricardo species, and the teeth appear to be somewhat shorter-crowned. In these characters the teeth from the Chanac seem to be more primitive than the type from the Ricardo formation. Other differences may be pointed out, as follows: The prefossette in the Chanac form is frequently open in the premolars, and may be open both lingually and posteriorly. In the lower teeth the protoconid and hypoconid may be separated by a canal, and the metastylid is often separate. In these characters the Chanac species seems to approach *H. mohavense callodonte* Merriam from the Ricardo (Merriam, 1919), but it differs in having fewer plications of the fossette borders, and especially in the enamel pattern of the lower molars.

The teeth from the Chanac are elongate anteroposteriorly, as may be seen in figure 5 and from the table of measurements. The mesostyle is heavier in the premolars than in the type of *H. mohavense*. In the milk molars the crowns are elongate and have a heavy deposit of cement, the fossettes are open in worn stages, and the length of crown is less than the anteroposterior diameter.

Additional as well as better specimens from the Chanac may demonstrate that the species from these deposits is distinct from *H. mohavense*. It may be more closely related to *H. mohavense callodonte*.

Measurements of dentition of Hipparion cf. mohavense (in millimeters)

Specimen no. (C.I.T. coll.)	Anteroposterior diameter	Transverse diameter	Length of protocone	Length of metaconid- metastylid column
1177, P ²	29.3	15.0	5.5
1178, P ²	28.9	16.4	5.5
1179, P ³	24.4	16.8	6.1
1180, P ⁴	27.4	17.6	6.7
2618, M ¹	24.1	15.9	5.5
2620, M ²	21.9	16.3	6.4
2623, M ₁	25.8	10.8	...	12.3
1176, P ₂	25.3	9.1	...	12.0
2628, P ₃	22.5	13.0	...	13.1
2622, P ₃	22.7	11.7	...	13.7

Nannippus cf. tehonensis (Merriam)

From the Chanac quarries come nine upper and four lower teeth which closely resemble comparable teeth of *Nannippus tehonensis* from the quarries lower in the stratigraphic section. It appears possible that this equid evolved from the species *N. tehonensis* during the period represented by the transitional beds between the Santa Margarita and the Chanac formations. Some constant features distinguish the two, but the characters do not seem of such importance as to merit specific separation.

The teeth are larger than those of *N. tehonensis*; they have a smaller and more rounded protocone; their fossettes are relatively wider transversely, but the difference is not great; they have a shallower posthypoconal valley. *Nannippus* sp., described by Stirton (Stirton, 1939b) from Univ. Calif. locality V3611, northeast of Moraga, Contra Costa County, is probably identical with the Chanac form.

A comparison of this form with similar types from the lower quarries suggests that in the evolution of the group a larger-crowned molar was developed. This appears to be at variance with the view that in later stages of time cheek teeth of *Nannippus* undergo reduction in size with increase in length of crown.

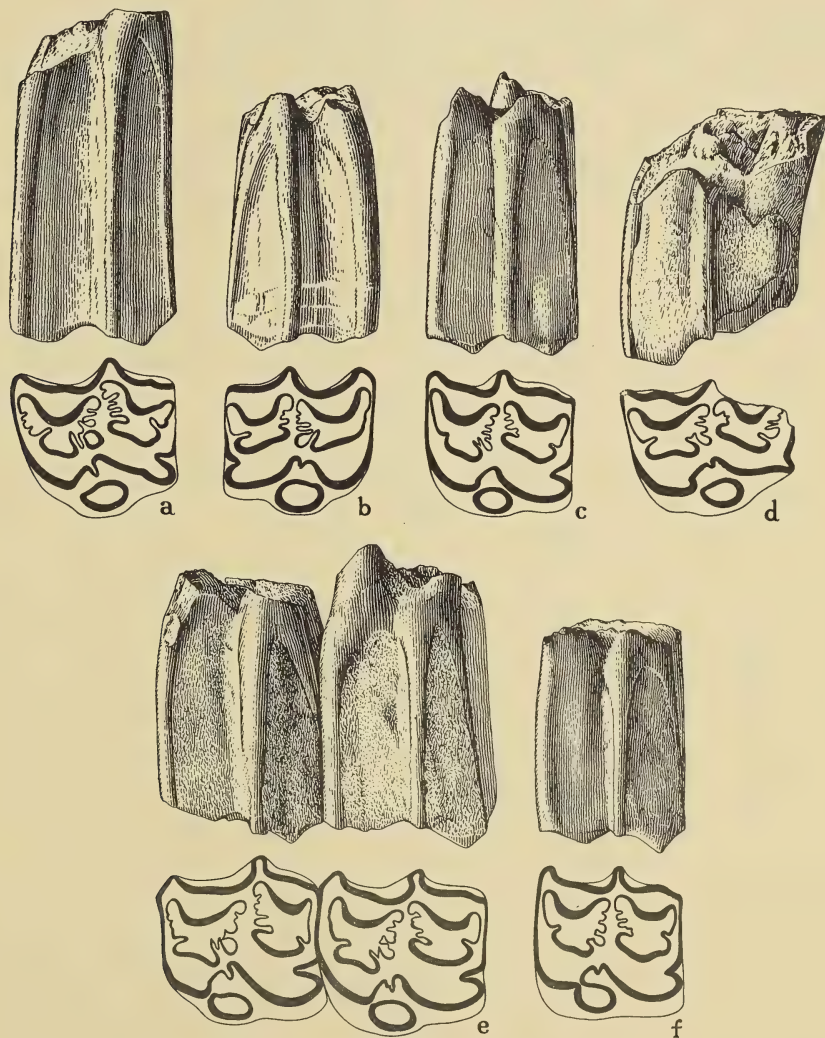


Fig. 6. *Nannippus* cf. *tehonensis* (Merriam). a, M¹, no. 1181; b, M¹, no. 1182; c, M¹, no. 1185; d, M³, no. 1184; e, P³, no. 1186; f, P³ and P⁴, no. 1183. Natural size. Calif. Inst. Tech. Vert. Pale. locality 104.

Measurements of dentition of Nannippus cf. tehonensis (in millimeters)

Specimen no. (C.I.T. coll.)	Anteroposterior diameter	Transverse diameter	Length of protocone	Length of metaconid- metastylid column
1183, P ³	21.1	17.3	6.4
1183, P ⁴	21.7	17.6	6.4
1181, M ¹	19.8	15.8	5.4
2624, M ³	19.4	13.2	4.9
2619, P ₃	22.4	12.8	...	13.0
2761, M ₁	20.1	11.9	...	12.4
2618, M ₂	22.5	10.5	...	12.6

Pliohippus leardi, n. sp.

Holotype. C.I.T. no. 2645, M¹, about one-fifth worn, from locality 302, Comanche Point; plate 2, figures 3, 3a, 3b.

Paratypes. C.I.T. no. 578, a composite series with P² to M³, about two-fifths worn, from locality 104, Comanche Point; plate 2, figure 1. C.I.T. no. 2650, P₃, locality 302; plate 3, figures 5, 5a, C.I.T. no. 2654, Dp³, locality 104; plate 2, figures 4, 4a, C.I.T. no. 2633, Dp₂-Dp₃, a slightly worn, complete set in lower jaw, from locality 305; plate 3, figures 1, 1a.

Teeth of this species are the most abundant specimens in the Chanac quarries. Unfortunately, in no instance was a complete dental series uncovered; in fact, only a few teeth were found associated. A sufficient number of upper teeth were obtained, however, to construct composite series, and many single teeth in all positions and stages of wear are available. No known fossil horses are identified with this form, and the type is therefore described as a new species. It is a pleasure to name the species for R. M. Leard, field collector for the California Institute of Technology.

Specific characters. The size of the molars is like that in *Pliohippus nobilis* Osborn, or larger in unworn teeth. The cheek teeth are long-crowned and moderately curved, with a very strong taper toward the root region associated with pronounced changes in enamel pattern. The protocone, which in unworn teeth is elongated and lenticular, with flattened buccal side, and is connected with the protoconule by a very narrow isthmus, becomes rounded and more strongly connected with increased wear. Although this change follows normally with wear, it is usually not so marked in other species. The tapering of the crown is so pronounced that the tooth diminishes to three-fourths or less of its original size after extreme wear. This feature is most evident in the molars, less so in the premolars. In the upper teeth the fossettes are simple; a single pli caballin is present; the hypocone is small with no lingual constriction. The teeth are squarish after wear, and heavily cemented; there is a prominent pli crochet in most teeth in early stages of wear; occasionally there is a small plication in back of the postfossette; the fossettes are sometimes connected; the prefossette is sometimes open internally in early stages. One prominent single fold enters the postfossette from the median portion of the metaloph,

and another enters the prefossette opposite the pli caballin; the hypoconal valley does not remain distinct, but disappears with wear. The lower molars are very long and straight, with distinctly separated metaconid and metastylid and prominent external valley. The premolars are much heavier than the molars; the protoconid and hypoconid have rounded external faces; there is a moderate postero-external style; the entostylid is swollen. The milk teeth have less cement and much shorter crowns than the permanent teeth.

A number of limb elements are assigned to *Pliohippus leardi* on the basis of size and proportions, but no diagnostic characters were observed.

Comparisons. The pronounced tapering of the crown toward the root region of the upper molars, and the decided changes which take place in size and in enamel pattern with wear, require recognition of similar stages of wear when comparisons are made between *P. leardi* and other species. Since many of the figured and described specimens are not moderately worn or unworn teeth, it is possible that

Measurements of dentition of Pliohippus leardi (in millimeters)

Specimen no. (C.I.T. coll.)	Anteroposterior diameter	Transverse diameter	Length of protocone	Height of crown	Length of metaconid- metastylid column
578, P ₂ *.....	34.7	21.6	7.2
578, P ₃ *.....	28.1	22.6	7.3
578, P ₄ *.....	28.6	22.8	7.6
578, M ₁ *.....	26.9	22.7	8.5
578, M ₂ *.....	27.5	21.4	8.4
578, M ₃ *.....	26.9	19.9	9.7
2642, P ₂	34.8	23.0	8.7	50.5
2638, P ₃	30.7	23.6	9.7	64.8
2660, P ₄	30.8	21.7	11.1	68.5
2658, M ₁	30.5	20.7	9.9	71.5
2659, M ₂	31.9	21.8	9.7	70.6
2647, M ₃	27.1	19.1	9.8	62.5a
2762, P ₂	31.8	11.3	10.5
2650, P ₃	30.5	15.1	69.0	12.1
2650, P ₄	31.7	14.6	71.0a	13.4
2673, M ₁	27.7	12.4	10.7
2673, M ₃	32.9	11.3	59.0a	10.0
2633, Dp ₂	37.6	8.9	2657 25.0a	14.7
2633, Dp ₃	33.6	11.6	2657 32.0a	14.0
2633, Dp ₄	34.5	10.7	2636 33.0a	12.7

* About half worn.

a, approximate.

future examination of such teeth may demonstrate relations between species already described and that occurring at the Tejon Hills. At present five species are known to be sufficiently close to the Chanac type to deserve comparison here.

Pliohippus leardi most closely resembles *P. nobilis* Osborn, from Long Island, Kansas. It differs in the following details: Although unworn cheek teeth are a little larger, the pronounced tapering of the crown soon reduces the size to such an extent that for most of its wear the crown size is actually smaller than in *P. nobilis*. The protocone does not become united with the hypocone until ex-

treme wear takes place; this cusp is more elongate at first and has a flat buccal side; later the protocone becomes rounded in the premolars and oval in the molars. The fossettes in the molar teeth are not so expanded as in *P. nobilis*.

As compared with *P. supremus* Leidy from South Dakota, the Chanac form is larger, and the upper cheek teeth of the latter have more curved crowns with slightly larger protocone. The teeth are more elongate; the para- and mesostyles seem more prominent; the fossettes are not open; the hypocone has no lingual indentation.

Teeth of *P. leidyani* Osborn from the Snake Creek beds are considerably smaller and slightly less hypsodont, and have less pronounced tapering of the crown. Moreover, the enamel pattern is more complicated, especially in the lower molars, and the hypocone is set off more strongly by an indentation on the lingual side.

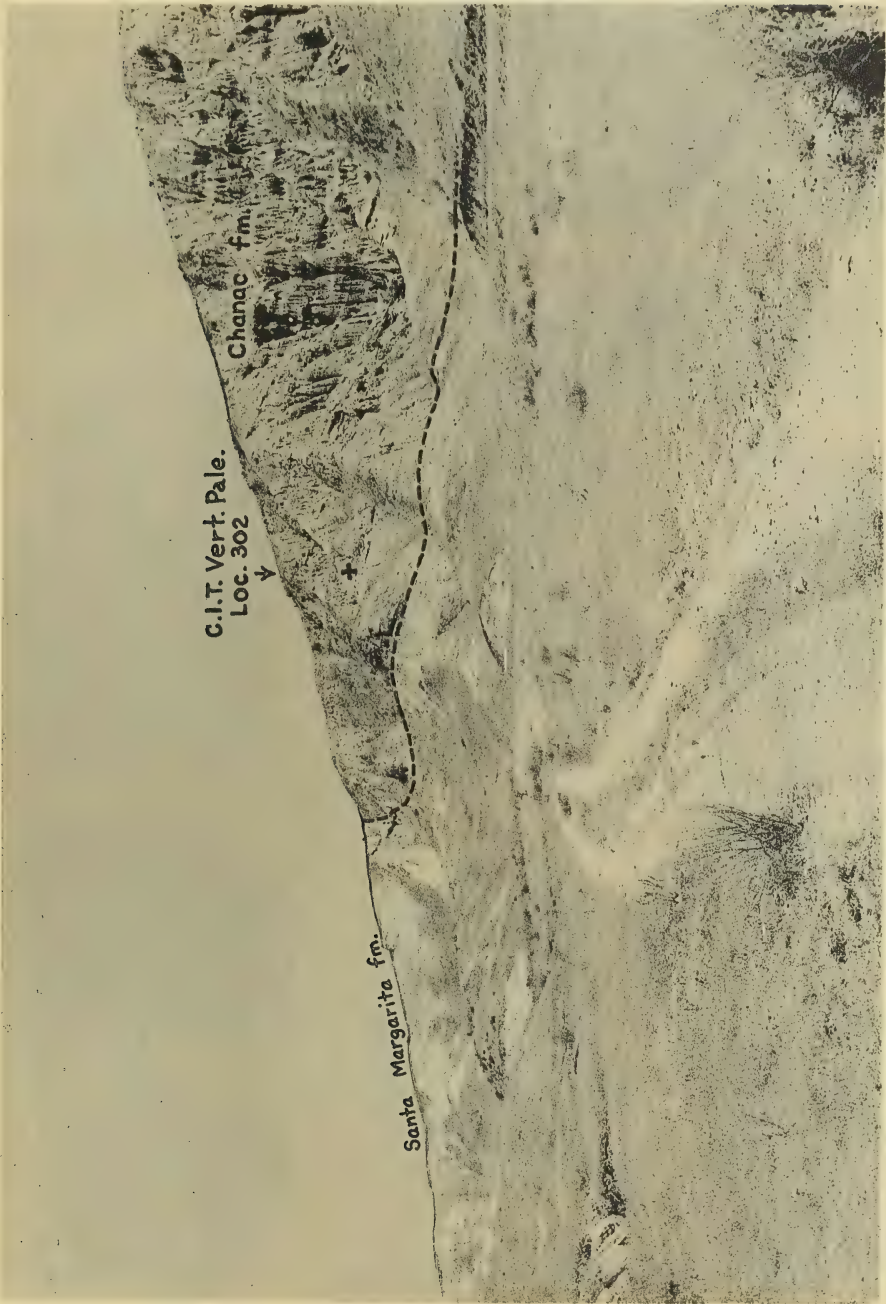
Plihippus tantalus Merriam from the Ricardo formation (Merriam, 1913) differs in smaller size. The fossettes are larger and their borders more complicated.

Plihippus cf. *interpolatus*, recently described from the Pinole tuff (Stirton, 1939b), is smaller with a somewhat different protocone and hypocone. A hypoconal lake is also present, a feature not observed in *P. leardi*.

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View looking east in northern part of Tejon Hills, Kern County, California, showing disconformable contact between the soft, white to gray, coarse, granitic sandstones of the marine Santa Margarita formation and the overlying buff, coarse, cross-bedded, ill sorted Chanac fanglomerates.

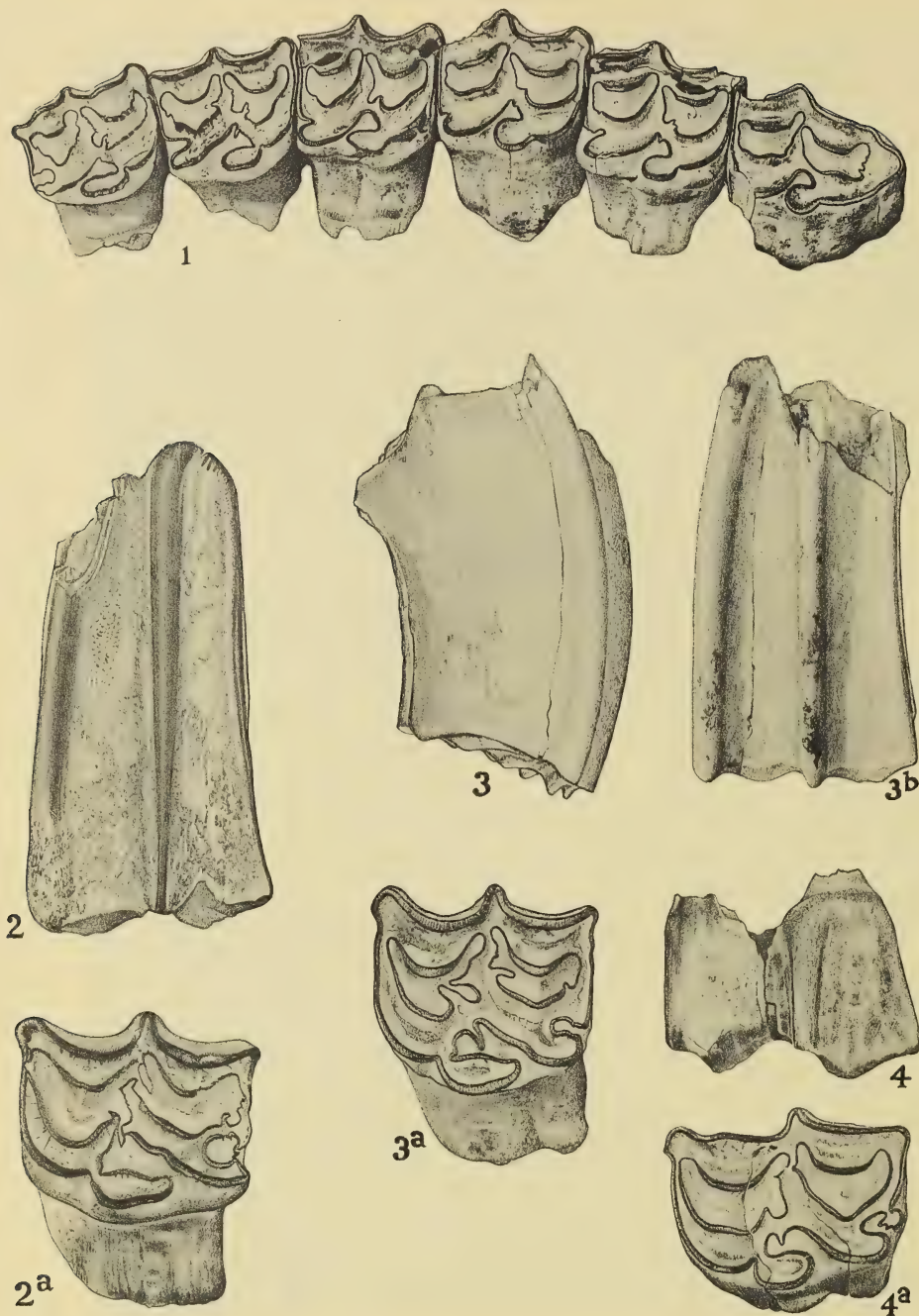
*Pliohippus leardi*, n. sp.

FIG. 1. No. 578, paratype, composite upper cheek-tooth series, occlusal view. $\times \frac{2}{3}$.

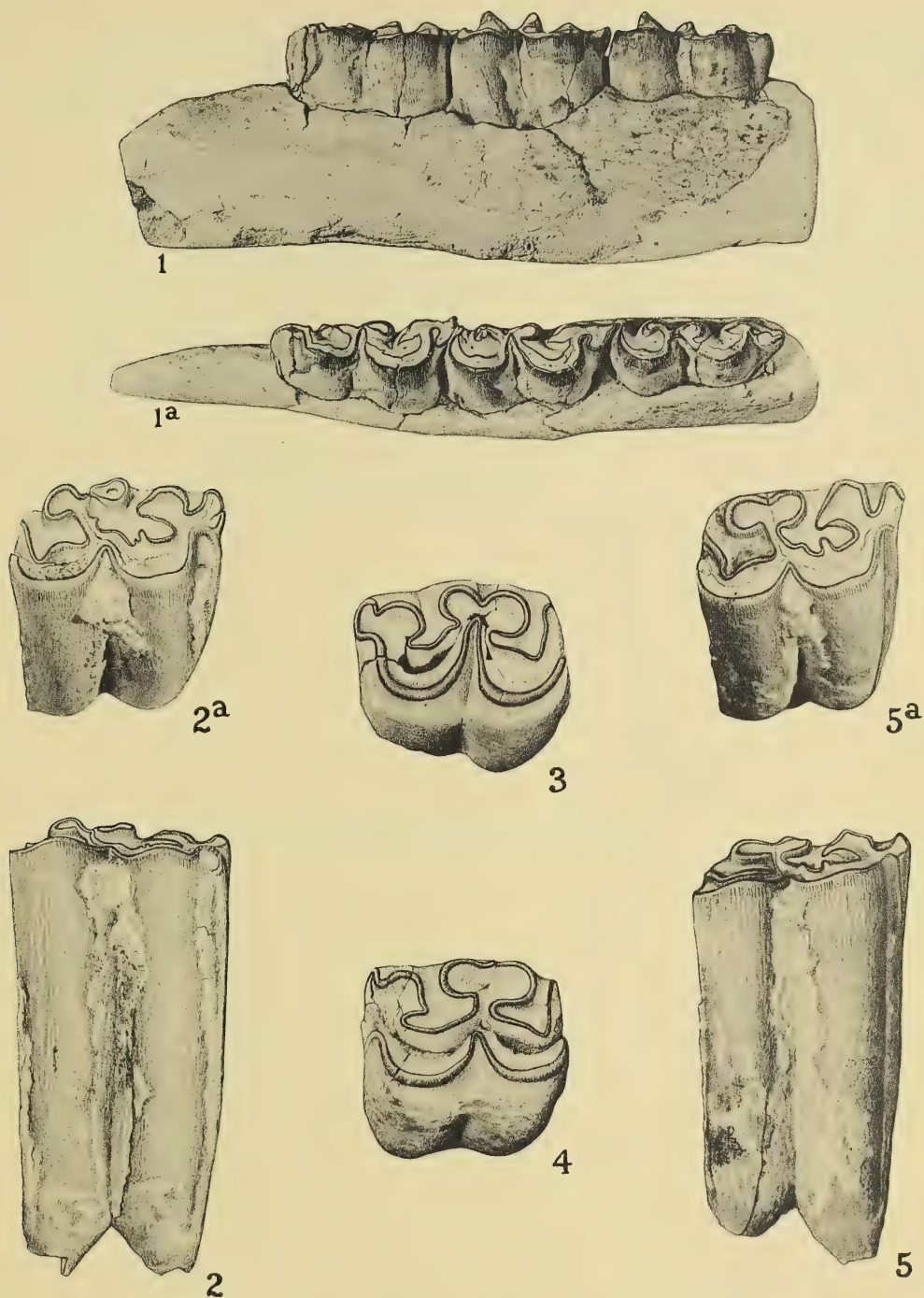
FIGS. 2, 2a. No. 2660, P^4 , lateral and occlusal views. $\times 1$.

FIGS. 3, 3a, 3b. No. 2645, holotype, M^1 , anterior, occlusal, and lateral views. $\times 1$.

FIGS. 4, 4a. No. 2654, paratype, Dp^3 , lateral and occlusal views. $\times 1$.

Calif. Inst. Tech. Vert. Pale. Coll.

Lower Pliocene, Tejon Hills, Kern County, California



Pliohippus leardi, n. sp.

FIGS. 1, 1a. No. 2633, paratype, Dp₂-Dp₄, lateral and occlusal views. $\times \frac{2}{3}$.

FIGS. 2, 2a. No. 2650, paratype, M₁, lateral and occlusal views. $\times 1$.

FIG. 3. No. 2674, P₄, occlusal view. $\times 1$.

FIG. 4. No. 2805, P₄, occlusal view. $\times 1$.

FIGS. 5, 5a. No. 2650, paratype, P₃, lateral and occlusal views. $\times 1$.

Calif. Inst. Tech. Vert. Pale. Coll.

Lower Pliocene, Tejon Hills, Kern County, California

CONTRIBUTIONS TO PALEONTOLOGY

II

A NEW PLIOCENE ANTELOPE FROM MEXICO
WITH REMARKS ON SOME KNOWN ANTILOCAPRIDS

E. L. FURLONG

With two plates and one text figure

[Issued May 1, 1941]

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A NEW PLIOCENE ANTELOPE FROM MEXICO
WITH REMARKS ON SOME KNOWN ANTILOCAPRIDS

Introduction

In the paleontological collections of the California Institute of Technology are remains of a new antelope recently collected with a Pliocene mammalian assemblage (Rincon fauna) in northern Mexico. Through the kindness of Dr. Chester Stock this material has been allocated to the author for description. There are likewise now available specimens of the antilocaprid genera *Ilingoceros* and *Sphenophalos* which have remained undescribed. Opportunity is therefore taken in the present paper to make some further observations on these forms, especially with regard to *Ilingoceros*.

Appreciation is expressed to Dr. J. C. Merriam, who originally described and discussed the relationships of *Ilingoceros* and *Sphenophalos*, for his continued interest in and support of the research on the fossil Antilocapridae.

*Hexobelomeryx*¹ *fricki*, n. gen. and n. sp.

(Plate 1, figures 2, 4, 5; plate 2)

Type specimen. C.I.T. no. 2780, a frontlet with horn cores partially preserved on both sides (pl. 1, fig. 2).

Paratypes. C.I.T. nos. 2769, 2771, and 2772, horn cores; nos. 2761, 2787, and 2799, upper and lower dentitions.

Locality. C.I.T. Vert. Pale. locality 291; Rincon Pliocene deposits, western Chihuahua, Mexico.

Generic and specific characters. The horn cores are not supraorbital as in *Antilocapra americana* and *Stockoceros*; only the anterior part of the base reaches above the posterior part of the orbit. The horn core is broad anteroposteriorly above the solid frontal base. Rising from a common base is a fork with two prongs or tines, and in addition a third prong, which usually projects anteriorly, sometimes posteriorly. The cleft between the tines of the fork is narrower than that between the fork and the third prong. The bottom of the cleft between the tines has a variable position above the base of the horn core, sometimes well above, at other times only a relatively short distance above. Of the three prongs, the anterior shows the largest cross section; the remaining two have cross sections of subequal size. When viewed from above, the middle prong is seen to project inward farther than either the anterior or the posterior prong.

¹ἑξ (*hex*), six; ὀβελός (*obelos*), a pointed object; μῆρυξ (*meryx*), a ruminant.

Anteroventral portion of orbital rim situated above M^3 ; superior cheek-tooth series short; root of M^3 reaching almost to malar-maxillary suture. Teeth hypsodont. Rami relatively short; diastema short, deep dorsoventrally at M_3 .

Description. The horn cores of *Hexobelomeryx* are not supraorbital in position as in *Merycodus*, *Sphenophalos*, *Stockoceros*, or *Antilocapra*. In other words, their base does not extend so far forward with reference to the orbit as in the genera mentioned. The horn core itself is of most peculiar type and not like any corresponding structure seen in antelopes previously described from the North American Tertiary. Rising from a single, anteroposteriorly elongated base (pl. 1, fig. 5), the horn core gives rise to a forward prong and a posterior fork of two prongs. The border of the cleft between the forward prong and the fork forms approximately a right angle. The forward prong is large and swings outward, upward, and forward. The fork consists of two prongs, the posterior of which swings outward, upward, and backward. The anterior prong of the fork is directed inward, upward, and backward (pl. 1, fig. 4). The cleft between the two prongs of the fork is much compressed and has a variable position above the base of the horn core. Of the several types of antelope horn core described by Childs Frick, none seems to correspond closely to this from the Rincon Pliocene. In *Texoceras* and in *Hayoceras*, for example, the horns appear to be of simpler construction than in the Mexican genus, and more like those in *Tetrameryx* or *Stockoceros* in this respect.

A curious anomaly occurs in the horn cores of this form from Mexico. Usually the largest of the three prongs of each horn core projects forward. This is the case in the type specimen, no. 2780, and in most of the additional horn-core material from the Rincon. In two well preserved specimens, nos. 2779 and 2772, however, the prong, which is distinct from the two comprising the fork, has a posterior position and projects backward (pl. 2, fig. 3). So different are these two horn cores from the usual type that one may question whether all the specimens can be referred to a single form. The view that all the horn cores belong to a single species and that the anomalous specimens probably represent curious variations from the norm is suggested in this paper. The following evidence may be marshaled to support this view: (1) The basic type of horn core is essentially the same in all specimens; in the variant, only the anterior prong is transposed; (2) no structural differences appear in the skeletal parts or in the dentition to warrant a separation of the antelope material into two groups; and (3) type and variant occur at the same locality. Furthermore, in the mammalian assemblage associated with *Hexobelomeryx*, as represented by the collection obtained from the several localities in the Rincon deposits, there is thus far no basis for establishing more than one faunal horizon.

Measurements of horn cores of Hexobelomeryx fricki (in millimeters)

S, specimen number (C.I.T. Coll.).

AP, anteroposterior diameter of constriction at base of antlers above orbit.

T, transverse diameter above orbits.

Loc. 275			Loc. 276			Loc. 277			Loc. 289			Loc. 291		
S	AP	T	S	AP	T	S	AP	T	S	AP	T	S	AP	T
2765..42.2	27.0		2770..43.0	22.3		2772..43.6	24.0		2774..40.7	19.5		2779..61.0	32.0	
2764..41.9	24.0		2771..41.0	25.3					2773..48.0	28.0		2780..45.3	23.5	
2766..48.5	29.6		2769..40.8	24.3					2776..46.0	22.5				
2768..41.2	23.0								2775..41.5	18.0				
									2777..43.0	22.0				
									2778..45.0	23.0				

The supraorbital foramen in the frontal is situated anterior to and on the median side of the horn core. Between the supraorbital foramina the frontal appears convex, in which respect it differs from that in *Antilocapra americana*. The anteroventral part of the orbital rim is situated above the last molar, and is therefore placed farther forward than in the modern pronghorn. The external opening of the infraorbital canal has a position above P^2 as in *Antilocapra*. The posterior part of the horn cores, the position of M^3 below the anteroventral portion of the orbital rim, and the shortened cheek-tooth series suggest a shortening of the facial part of the skull.

The horizontal ramus is deep below M_3 (pl. 2, figs. 1, 2). Anteriorly, the depth decreases toward the diastemal portion of the jaw more rapidly than in *Antilocapra*. The ramus is heavier and deeper than in *Stockoceros conklingi*. The depth of the ramus at the posterior end of M_3 ranges from 30 to 37 mm. in *Hexobelomeryx*. In *Stockoceros conklingi* the comparable measurement of a ramus of maximum size is 28 mm. The masseteric ridge, situated near the ventral border and immediately behind the level of M_3 , is much more strongly developed than in *Antilocapra*. The diastema between the anterior premolar and the incisors is short.

The cheek teeth are hypsodont. In both upper and lower premolar series P_2 - P_4 are present, although in several rami (for example, no. 2787, pl. 2, fig. 2) the premolars are reduced to P_3 - P_4 . P_4 is smaller in proportion to the molar teeth in *Hexobelomeryx* (pl. 2, fig. 5) than in *Antilocapra*. This tooth has the characteristic half-molar pattern, the inner crescent being completely formed. In P_3 a broad groove on the inner side demarcates the anterointernal crest from the principal cusp. A small groove of limited vertical extent occurs behind the principal cusp. At the posteroexternal angle of the crown a style is formed, its presence being accentuated by the shallow vertical groove in front of it. The same type of crown construction is present in P_4 except that the styles at the anterointernal and posteroexternal corners of the crown are stronger. M_3 is usually a three-lobed tooth, but in no. 2799 (pl. 2, fig. 1), because of

lengthening out of the posterior part of the crown, four lobes are present.

Measurements of dentition (in millimeters)

<i>Hexobelomeryx</i>				<i>Stockoceros</i>			
C. I. T. no.	P ₂ -P ₄ inc.	M ₁ -M ₃ inc.	P ₂ -M ₃ inc.	C. I. T. no.	P ₂ -P ₄ inc.	M ₁ -M ₃ inc.	P ₂ -M ₃ inc.
2785	16.3	50.0	65.4	2931	22.0	47.3	69.0
2786	15.0	50.0	65.9	2932	20.2	40.4	61.5
2787 (P ₃ -P ₄)....	15.0	44.0	60.9	2933	21.5	41.4	64.0
2788	20.6	46.0	61.0a	2934	21.0	41.2	62.3
2789 (P ₃ -P ₄)....	12.4	47.9	61.3	2935	22.0	39.0	61.8
2790	16.0a	44.0a	61.0	2936	25.0	43.0	67.0
2791	17.3	47.0	67.0	2937	20.8	38.8	60.5
2792	21.2	44.5	66.5	2938	21.5	38.2	62.0
2793	18.0	44.2	62.5	2939	21.3	41.4	64.2
2794	18.0	44.6	64.3	2940	21.0	40.0	63.0
2799	18.0	47.3	65.0	2941	20.5	39.3	61.5
2800	14.9	43.5	57.3	2942	19.0	44.2	65.0
Averages.....	16.7	46.1	63.2	21.2	41.2	63.5

a, approximate.

Few rami of *Hexobelomeryx* are complete anterior to the third incisor. In those that are complete, the length of the diastema ranges from 42 to 51 mm. In *Stockoceros conklingi* the length ranges from 47 to 65 mm.

Length of diastema between I₃ and P₂ (in millimeters)

<i>Hexobelomeryx</i>		<i>Stockoceros</i>	
C. I. T. no.	Length of diastema	C. I. T. no.	Length of diastema
2785	2931	61.9
2786	2932	62.0
2787	2933	62.0
2788	2934	65.0
2789	46.9a	2935	62.0
2790	47.8	2936	60.9
2791	2937	65.0
2792	2938	50.3
2793	2939	59.0a
2794	45.5	2940	59.2
2799	47.0	2941
2800	47.0	2942	58.2

a, approximate.

Ilingoceros alexandrae Merriam

(Plate 1, figure 1)

Among numerous fragmentary horn cores and skeletal parts of *Ilingoceros alexandrae* found in the Thousand Creek Middle Pliocene of Nevada is the frontlet of a skull, C.I.T. Vert. Pale. Coll. no. 494, from locality 63, shown in plate 1, figure 1. The inner, superior faces of the orbits are present. The twisted horn cores rise immediately above the supraorbital foramina and orbits. The frontal bone is broken near the line of the anterior parietal suture and across the forehead in line with the supraorbital foramina. The bone between the horn cores is relatively thick and ventrally shows a part of the inner surface of the brain case.

Orienting the frontlet on the basis of the orbital parts that are present, it is seen that the horn cores incline backward and outward. Thus, the attitude of the horn core in *Ilingoceros* is noticeably different from that in *Sphenophalos* and *Antilocapra*. There is no abrupt depression of the frontals between the supraorbital foramina as in *Antilocapra americana* or in *Sphenophalos*.

The parts of horn-core shafts present above and behind the orbits are (right) 107.0 mm. and (left) 111.0 mm. long. The truncated distal ends of the cores project laterally 48.0 mm. beyond the orbital rims. The greatest diameter of the first spiral above the base is 29.0 mm., that of the second spiral 33.5 mm. As the spirals show no diminution in size distally, no estimate of complete length or character of termination can be made.

Merriam² in discussing the probable relationships of *I. alexandrae* suggested that it belonged in a new family. Childs Frick³ in his classification of the horned ruminants has erected the subfamily Ilingocerotinae for this genus.

A relation between *I. alexandrae* and *S. nevadanus* has been suggested on the basis of morphology of horn-core structure. The tight spiral twist in *Ilingoceros* horn cores, however, differs decidedly from the slight twist outward of the anterior tine in *Sphenophalos*. The horn cores of *Sphenophalos*, with their broad anteroposterior diameter, are not comparable to those of *Ilingoceros*, with their cylindrical proximal ends. C.I.T. specimen 597 (pl. 1, fig. 3), belonging to a very young individual of *Sphenophalos*, shows no tendency to develop a spiral structure. In C.I.T. no. 494 (*Ilingoceros*), the dorsoventral axis of the horn core is situated above the posterior end of the orbit; in *Sphenophalos* it lies over the middle of the orbit. The long

²J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 5, pp. 319-330, 1909; *ibid.*, vol. 6, pp. 302-303, 1911.

³C. Frick, Bull. Amer. Mus. Nat. Hist., vol. 69, p. 469, 1937.

axis of the core normal to the former axis in *Ilingoceros* (no. 494) extends through the supraorbital foramina, whereas in *Sphenophalos* it lies above the anteroorbital rim. The positions of the supraorbital foramina in relation to the base of the horn core are very different in the two genera. On the other hand, the foramina open into the orbits in the same way. The position of the supraorbital foramina in *Sphenophalos* is comparable to that in *Stockoceros conklingi*, *Tetrameryx*, and *Antilocapra americana*.

Stirton⁴ states that on the basis of available evidence it has not been shown that the genus *Plioceros* Frick differs from *Sphenophalos*. The geographic distribution as well as stratigraphic occurrence of the former genus might have some bearing on the matter.

No horn cores of *Ilingoceros* have been found at any C.I.T. locality where *Sphenophalos* remains occur, with the one exception of the original Thousand Creek locality. It appears highly improbable that sex dimorphism accounts for the difference between the horn cores of the two genera.

So far, no remains of *Ilingoceros* are recorded from any but the type locality in Thousand Creek, Nevada. The genus *Sphenophalos* has a much wider geographical distribution through the Great Basin province. If *Plioceros* is congeneric with *Sphenophalos* and has a similar geological age, the range of *Sphenophalos* may include areas in Nebraska and New Mexico.

Conclusions

To the extraordinary number and variety of antilocaprids from the later Cenozoic deposits of North America is added a new genus, *Hexobelomeryx*. This type from the middle Pliocene of northern Mexico shows an unusual type of specialization of its horn cores, in which three distinct prongs are present.

Discovery of this form emphasizes the fact that the greatest diversity in the structure of the horn core is found among the antilocaprids of the later Pliocene. Unique among these are not only *Hexobelomeryx*, but also *Ilingoceros* from the Thousand Creek beds of Nevada.

⁴R. A. Stirton, Amer. Jour. Sci., ser. 5, vol. 24, pp. 46-51, 1932.

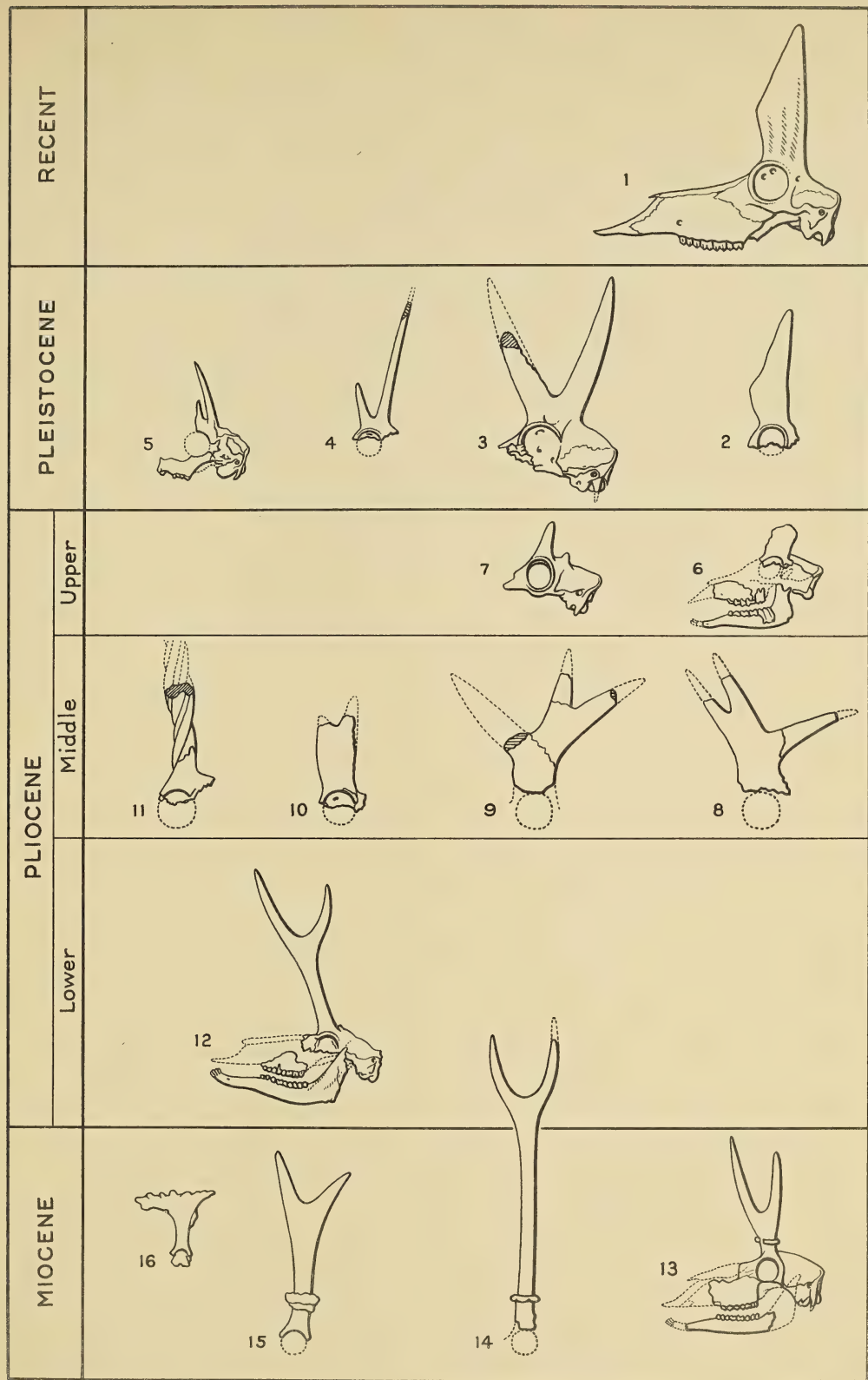


Fig. 1. Horn cores of recent and fossil American antelopes: (1) *Antilocapra americana* Ord; (2) *Antilocapra* cf. *americana* Ord; (3) *Stockoceros conklingi* (Stock); (4) *Tetrameryx schuleri* Lull; (5) *Capromeryx mexicana* Furlong; (6) *Proantilocapra platycornea* Barbour and Schultz; (7) *Ceratomeryx prentici* Gazin; (8) and (9) *Hexobelomeryx fricki* Furlong; (10) *Sphenophalos nevadanus* Merriam; (11) *Ilingoceros alexandrae* Merriam; (12) *Merycodus* cf. *furcatus* Leidy; (13) *Merycodus necatus* Leidy; (14) *Merycodus loxoceros* Furlong; (15) *Merycodus hookwayi* Furlong; (16) *Merriamoceras coronatus* Merriam. Greatly reduced.

PLATES

PLATE I

All specimens $\times 3/5$

FIG. 1. *Ilingoceros alexandrae* Merriam. No. 494, frontlet with horn cores. Thousand Creek Pliocene, Nevada.

FIG. 2. *Hexobelomeryx fricki*, n. gen. and n. sp. Type specimen, no. 2780, frontlet with bases of horn cores. Rincon Pliocene, Mexico.

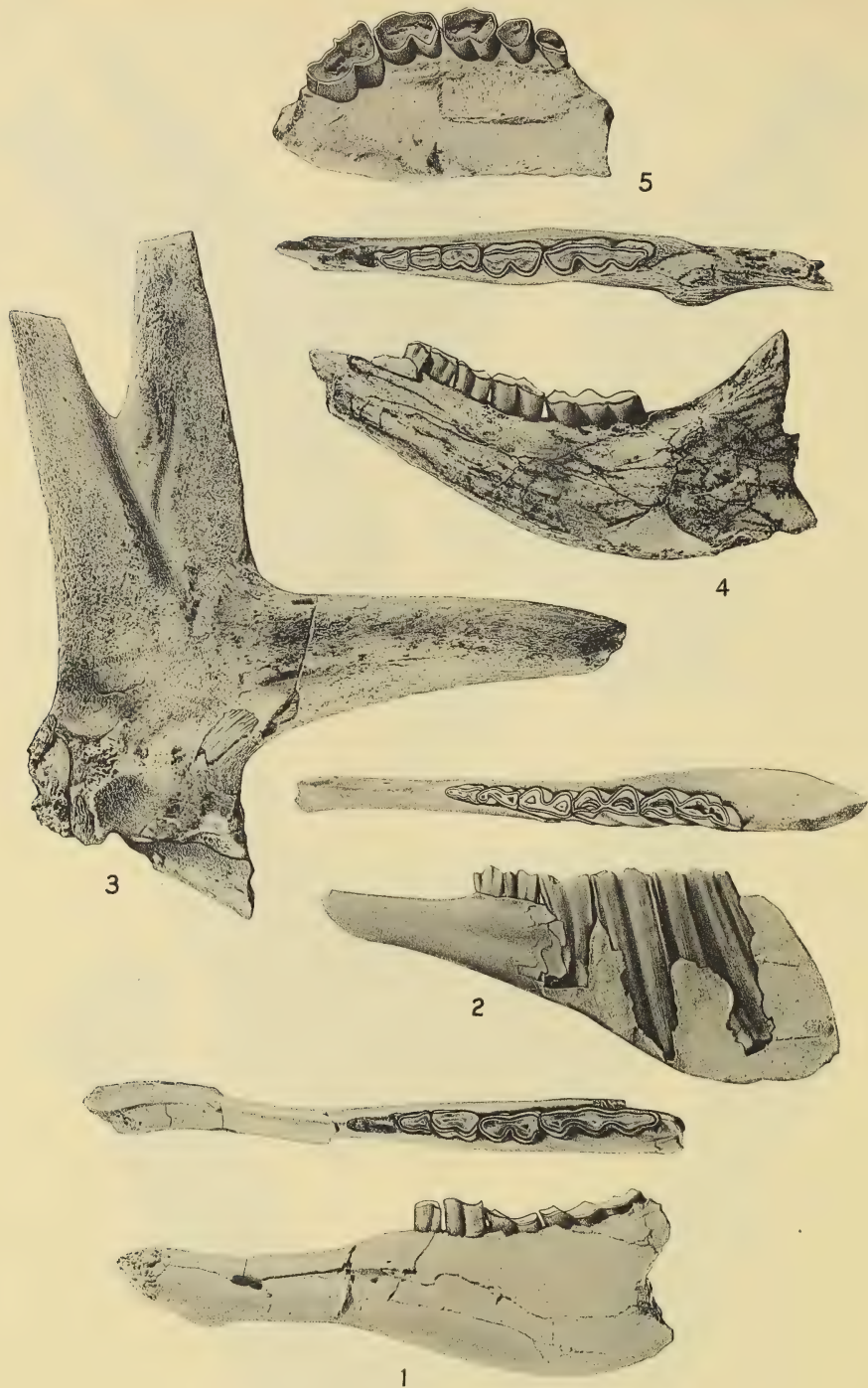
FIG. 3. *Sphenophalos* sp. No. 597, horn core of immature specimen. Thousand Creek Pliocene, Nevada.

FIG. 4. *Hexobelomeryx fricki*, n. gen. and n. sp. No. 2769, horn cores. Rincon Pliocene, Mexico.

FIG. 5. *Hexobelomeryx fricki*, n. gen. and n. sp. No. 2771, horn cores. Rincon Pliocene, Mexico.

Calif. Inst. Tech. Vert. Pale. Coll.





Hexobelomeryx fricki, n. gen. and n. sp.

All specimens $\times 3/5$

FIG. 1. No. 2799, ramus and lower dentition.

FIG. 2. No. 2787, ramus and lower dentition.

FIG. 3. No. 2772, horn cores.

FIG. 4. No. 2793, ramus and lower dentition.

FIG. 5. No. 2761, maxillary fragment with upper cheek teeth.

III

QUATERNARY BIRD LIFE OF THE MCKITTRICK ASPHALT,
CALIFORNIA

IDA S. DeMAY

With four text figures

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QUATERNARY BIRD LIFE OF THE MCKITTRICK ASPHALT, CALIFORNIA

INTRODUCTION

Fossil bird remains from the Quaternary asphaltic lenses near McKittrick, California have been discussed in a number of papers during the past twenty years. Two avifaunas in the collection of the University of California were described in detail by L. H. Miller (1925, 1935). The first of these included a large number of aquatic or semiaquatic species, and therefore presented a definite contrast with the Pleistocene avifauna of Rancho La Brea. The second consisted predominantly of birds of nonaquatic habitat, and showed greater similarity to that of the asphalt deposits in Los Angeles. In addition to a general account of the McKittrick avifaunas, special studies have appeared which relate to new species identified in the collections of the University of California (L. H. Miller, 1924, 1927).

Thus far no comprehensive study has been made of the McKittrick avifauna based on the collections of the California Institute of Technology, although certain species among the fossil birds have in the past received individual attention. For example, L. H. Miller described some stork material in 1932 and 1938. A new genus and species of pygmy goose was described by Ross in 1935, and the species was later reassigned by Howard (1936). In 1938, Howard also identified remains of the caracara. L. H. Miller (1935) states that his account of the avifauna from McKittrick is based on the remains in the collection of the University of California, but notes that an examination was likewise made of some of the bird bones in the collection of the California Institute of Technology.

Since the fossil materials in the collections of the latter institution represent the largest number of specimens thus far obtained at McKittrick, it seems desirable to survey this important Quaternary bird assemblage in order to determine additional facts regarding its constitution, and to establish its ecologic and age relationships. Fortunately, recent studies make available more information regarding the avifaunas of Rancho La Brea and Carpinteria, and thus furnish a basis for closer comparison between these and the McKittrick assemblage than has been possible heretofore.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge my indebtedness to Dr. Loye Holmes Miller, of the University of California at Los Angeles, for guidance and constant encouragement in the course of this study. Access to his comparative collections of Recent and fossil bird skeletons and free use of his documented materials have made this work possible.

The fossil bird bones from McKittrick in the collections of the California Institute of Technology were made available by Dr. Chester Stock, whose continued interest and valuable advice are deeply appreciated. Dr. Hildegard Howard very kindly permitted access to the comparative material in the Rancho

La Brea and Recent collections of the Los Angeles Museum. I should also like to extend thanks to Dr. Howard for suggestions and for aid in the identification of some of the more difficult species. The text figures were prepared by David P. Willoughby. Other acknowledgments are made in the text.

OCCURRENCE AND NATURE OF AVIFAUNA

The fossiliferous asphalt beds of McKittrick, located about a mile south of the village of that name, were discovered during construction work on the Taft-McKittrick highway through the oil fields southwest of Bakersfield, in western Kern County (Merriam and Stock, 1921). The Pleistocene vertebrate remains were uncovered on either side of the highway, and it is evident that the fossil-bearing deposits extend beneath the paved road. The original cut on the southeast side is Univ. Calif. locality 4096, and has been designated by L. H. Miller (1935) as McKittrick locality 1. McKittrick locality 2, on the northwest side of the road, is Univ. Calif. locality 7139, and corresponds to Calif. Inst. Tech. Coll. locality 138 (Schultz, 1938). The collection of fossil birds considered in this paper was taken from C.I.T. locality 138.

The asphalt deposits at McKittrick comprise a series of thin sheets of asphalt and fine-grained silt, resting unconformably upon the Santa Margarita and McKittrick formations. The Pleistocene lenses are exposed to a depth of about 10 feet, and are overlaid by a stratum containing bones of Recent mammals and birds (Schultz, 1938). A number of the latter seem to be included in the present collection.

A comparison of the two McKittrick assemblages of fossil birds described by Miller (1922, 1925, 1935) shows a marked contrast in the percentage of aquatic species present. In fauna 1, aquatic and semiaquatic species constitute two-thirds of the total. Half of these are anserines and the rest are shore birds and waders, all of which are usually found on mud flats or along the marshy edges of lakes and estuaries. The gulls and divers, however, are represented by only one bone, the femur of a pied-billed grebe. Unlike the anserines, these birds prefer the open water of bays and lakes, and are not generally found on small ponds and streams. Approximately one-third of the species are nonaquatic predators and other nonaquatic forms. It seems probable, therefore, that the oil seeps were located near the edge of a lake or pond. The fauna from locality 2 is more terrestrial in character, and, like that of Rancho La Brea, shows a preponderance of flesh-eaters. Nearly two-thirds of the species are nonaquatic predators, and about one-fourth are aquatic or semiaquatic birds (Miller, 1935).

The combined evidence of the mammals, birds, and plants indicates that the physical environment of the region in late Pleistocene time resembled that of today, except for slight changes in topography. The McKittrick region was probably an arid valley in the Lower Sonoran faunal zone, with an adjacent Upper Sonoran zone in the near-by hills. The saltbush (*Atriplex*

polycarpa), characteristic of the western parts of the San Joaquin Valley today, is found in the McKittrick asphalt. Associated today with the salt-bush formation is the sage sparrow (*Amphispiza belli*), which is known also from the Pleistocene deposit. The presence of California jays and of a few piñon pines indicates that the Upper Sonoran piñon forest, which now extends in the Coast Ranges to the vicinity of Mount Pinos in southern Kern County, was distributed farther north and east and to lower elevations in Pleistocene time. The lacustrine body that provided a habitat for the aquatic species found at McKittrick was probably much like the lakes which are found today in the arid parts of the San Joaquin Valley (A. H. Miller, 1937).

At Rancho La Brea the fauna and flora are largely characteristic of the Upper Sonoran-San Diegan region. Meadowlarks are more abundant than at McKittrick, and horned larks are less so. The pine forest association is almost absent, but live oaks and Lewis woodpeckers are present. Carpinteria was much more humid during the Pleistocene than it is at present. The asphalt deposits at this locality occurred in a coastal Transition forest such as is now found in the California fog belt. Monterey and Bishop pines and pygmy nuthatches are typical of the Carpinteria assemblage (A. H. Miller, 1937).

Many species of birds found at McKittrick have little value in determining the presence of particular life zones because of their wide distribution. Among these one may list the large raptors, which have only recently retreated southward, and the crows and ravens. A. H. Miller (1937) states that crows are entirely absent from the McKittrick collection described by him, although they occur in Rancho La Brea collections and are now found in the river bottom on the arid western side of the San Joaquin Valley. The extinct California turkey (**Parapavo californicus*),¹ so numerous at Rancho La Brea, does not occur in the McKittrick collections. Presumably not enough ground cover was available to furnish an adequate habitat for these large gallinaceous birds, although the occurrence of a body of water might well have brought them into the immediate region of the tar had they been present. Perhaps the mountain barrier which today exists between McKittrick and Rancho La Brea was even more formidable during Pleistocene time, preventing a migration of **Parapavo* from the Los Angeles coastal area into the San Joaquin Valley. A similar reason may account for the absence of **Wetmoregyps daggetti*, *Spizaetus grinnelli*, and perhaps *Morphnus woodwardi* (L. H. Miller, 1935).

¹Throughout this paper, the asterisk (*) indicates that the genus or species following it is extinct.

DISCUSSION OF SPECIES

Since most of the birds found at McKittrick belong to Recent species, and the extinct species have been previously described in detail, no descriptions are included in this paper. The arrangement of species follows that of the *Check-list of the fossil birds of North America* (Wetmore, 1940).

The method used in determining the number of individuals in each species is that described by Howard (1930). In making a census based upon the wing or leg bones, the left or right element occurring in greatest number in each species was taken, as a rule, to represent the minimum number of individuals present. Parts of broken bones were matched whenever possible, and counted as one bone; additional ends were counted as whole bones. It should be remembered, however, that many more individuals are probably represented in some species than the figures would indicate. For this reason, the total number of bones and bone fragments for each group is also given.

At least 2150 individual birds, including the unidentified anserines, shore birds, and small passerines, are recorded in the present census. Approximately 16,000 bones and bone fragments in the McKittrick collection of the California Institute are now identified. In addition, there remain an estimated total of 4600 unidentified bones, of which number perhaps 4000 belong to small passerines. The total number of identified bird bones in all the McKittrick collections is approximately 20,000.

COLYMBIFORMES (Grebes)

These diving birds prefer the open water of bays, estuaries, tule-bordered inland ponds, and sloughs (Hoffmann, 1927), but are sometimes found in small, shallow ponds or even in irrigation ditches. Miller (1925) suggests that the scarcity of grebe remains at McKittrick indicates that only shallow pools of water were present in the immediate vicinity of the tar seeps.

Podilymbus podiceps (Linnaeus). Pied-billed grebe

1 individual; 1 bone (tarsometatarsus).

This species is an abundant breeder at Buena Vista Lake today, but is represented in fauna 1 by a single bone (Miller, 1925). It is not recorded in fauna 2, and was probably a straggler in the region.

CICONIIFORMES (Storklike Birds)

Minimum number of individuals, 45.

Total number of bones and fragments, 485.

The herons and storks are inhabitants of marshes, reedy pools and ditches, mud flats, and the beaches of bays and estuaries (Hoffmann, 1927). Some of them are known to seek insects and small rodents in dry fields, and are therefore not to be regarded as strictly aquatic birds (Miller, 1935).

Ardea herodias Linnaeus. Great blue heron

8 individuals; 66 bones.

This heron is well represented in fauna 1, but only 15 bones of the species are found in fauna 2 (Miller, 1925, 1935). It is found at Buena Vista Lake today, and must have nested near the Pleistocene lake at McKittrick. This is indicated by the presence of incompletely ossified bones of young individuals in the collection.

Casmerodius albus (Gmelin). American egret

3 individuals; 7 bones.

The American egret has not been previously recorded from the McKittrick asphalt. Its rarity in this collection indicates that the birds were probably not very abundant in the region in Pleistocene time, but some of them apparently nested there.

Florida caerulea (Linnaeus) (?). Little blue heron

3 individuals; 8 bones.

Butorides virescens (Linnaeus) (?). Green heron

1 individual; 4 bones.

Nycticorax nycticorax (Linnaeus). Black-crowned night heron

1 individual; 5 bones.

Neither the little blue heron nor the green heron has been previously found in the McKittrick asphalt, and the night heron was previously known by a single bone. The little blue heron is identified tentatively because of the scarcity of the fossil material and because of a possible confusion with *Hydranassa tricolor*. Identification of the green heron is made tentatively since the bones show slight differences when compared with available Recent material. Two of these herons are found at Buena Vista Lake today.

*Ciconia *maltha* Miller. Asphalt stork

29 individuals; 395 bones.

One hundred and seven bones of this extinct stork occur in fauna 2. This species shows considerable variation in size, as noted by Miller in 1932. He states that the size range extends beyond that of *Jabiru* and *Euxenura* at either end of the series, and that *Ciconia *maltha* differs from these species in many details of structure (Miller, 1910, 1932). Young individuals occur in the present collection.

ANSERIFORMES (Gooselike Birds)

Minimum number of individuals, 183.

Total identified bones and fragments, 1628.

Ducks and geese commonly feed along the marshy edges of lakes, ponds, shallow bays, and estuaries. Geese may also feed in grain fields near by, but some of the ducks prefer to dive for food in open water.

Branta canadensis (Linnaeus). Canada goose

3 individuals; 26 bones.

Five bones of this species, all stouter than those of the Recent goose, were found at locality 2. In the avifauna from locality 138, only one bone, the proximal end of a tibiotarsus, is stouter than the comparable element in Recent species.

**Anabernicula minuscula* (Wetmore). Brea pygmy goose

11 individuals; 99 bones.

This small goose was described from McKittrick by Ross (1935), who named it **Anabernicula gracilenta*. He states that it shows characters of both the ducks and the geese, but is more slender than any living goose. In 1936, Howard referred to this genus a humerus described by Wetmore from the Pleistocene of Arizona, and a number of bones from Rancho La Brea. The species **gracilenta* is now regarded as synonymous with Wetmore's **minuscula*.

Anas platyrhynchos Linnaeus. Mallard

36 individuals; 527 bones.

Ninety-two specimens of this very adaptable species are identified in fauna 2.

Chaulelasmus streperus (Linnaeus). Gadwall

7 individuals; 31 bones.

Mareca americana (Gmelin). Baldpate

8 individuals; 56 bones.

Dafila acuta (Linnaeus). Pintail

6 individuals; 24 bones.

The gadwall is represented in fauna 2 by 5 bones, and the baldpate by 7 bones. Only one perfect tibiotarsus of the baldpate and several bones referable to the pintail occur in fauna 1.

Nettion carolinense (Gmelin). Green-winged teal.

42 individuals; 355 bones.

Next to the golden eagle, this species is represented by the largest number of bones in the collection of fauna 1. In fauna 2, however, the green-winged teal is known by only 34 bones. These teals are very adaptable, and frequent small puddles as well as large bodies of water.

Querquedula cyanoptera (Vieillot). Cinnamon teal

31 individuals; 403 bones.

Spatula clypeata (Linnaeus). Shoveler

6 individuals; 33 bones.

The cinnamon teal is abundant in fauna 1, and 81 bones are known in fauna 2. The shoveler duck, on the other hand, is represented by only two or three bones

in the two collections. These ducks feed by dabbling in shallow water near the edges of sloughs and marshes.

Nyroca americana (Eyton). Redhead

7 individuals; 33 bones.

Nyroca affinis (Eyton). Lesser scaup duck

3 individuals; 10 bones.

Charitonetta albeola (Linnaeus). Bufflehead

3 individuals; 31 bones.

The last three species are poorly represented in the McKittrick collections. This is due perhaps to the fact that these ducks prefer the open waters of lakes or bays, where they dive for food.

Unidentified Anseriformes

More than 140 bones of ducks and geese are not identified as to genus and species. These represent at least 20 individuals.

FALCONIFORMES (Falconlike Birds)

Minimum number of individuals, 675.

Total identified bones and fragments, 7806.

This order includes the vultures and condors, which are carrion feeders of such widely diverse habitats as to have little value as life-zone indicators. Their habit of alighting on the ground and approaching their food on foot may account for the scarcity of these birds in the McKittrick deposits. Some of the hawks, such as the sharp-shinned and Cooper's hawks and the falcons, are hunters of open country. The bald eagle is seldom found far from the ocean or from large lakes. This may be one reason for its scarcity at McKittrick. The golden eagle is often seen soaring above the foothills and mountains inland as well as along the coast. These birds may have become entangled in the tar when they dropped down upon a partly submerged carcass and by accident permitted their wings or feet to come in contact with the sticky tar in their struggles with the prey (Hoffmann, 1927; Miller, 1935).

Cathartes aura (Linnaeus). Turkey vulture

7 individuals; 67 bones.

*Coragyps *occidentalis* (Miller). Western black vulture

4 individuals; 32 bones.

Cathartes aura, the only small vulture now living in southern California, outnumbered the extinct *Coragyps* by more than five to one in fauna 2, but the reverse is the case at Rancho La Brea (Howard, 1930; Miller, 1935). Only 4 bones of the western black vulture have been previously found at McKittrick, and Miller has suggested that latitude may have been a factor in accounting for their scarcity. In the present collection *Cathartes* outnumbers *Coragyps* by approximately two to one. *Coragyps *occidentalis* is a somewhat larger

and stouter bird than the living black vulture (*C. atratus*), according to the original description by Miller in 1909. The femur is longer and heavier, the tibiotarsus is shorter and stouter, the foot is wider, and the humerus is longer.

Gymnogyps californianus (Shaw). California condor

2 individuals; 11 bones.

These are the first condor bones to be recorded from the McKittrick Pleistocene. The specimens are slightly larger than comparable Recent bones of California condors in Dr. Miller's collection and differ from them in several details. When, however, comparisons are made with the large series of specimens of condors from the Rancho La Brea Pleistocene, the McKittrick bones are seen to fall within the range of variability of the species. Miller (1935) has commented on the absence of condors in previous McKittrick collections. These birds were widely distributed in Pleistocene time, and their range even today includes the southwestern San Joaquin Valley region. Why, then, are their remains so scarce in the McKittrick asphalt?

**Teratornis merriami* Miller. Merriam's teratorn

8 individuals; 124 bones.

This gigantic bird shows a combination of eagle- and vulturelike characters, having a skull much larger than that of the condor, and a bill higher and more like that of the eagle. With a wingspread of possibly 16 to 18 feet, **Teratornis* was one of the largest birds of flight known (Miller, 1909; Stock, 1930). Three bones of this species occur in fauna 1, and 178 in fauna 2. It should be noted that remains of **Teratornis* are less abundant in the present assemblage than in fauna 2, even though the former collection is four or five times larger than the latter. A comparable decrease is also found in the number of large vultures and eagles. Possibly this change reflects a decrease in number of these birds toward the end of Pleistocene and the beginning of Recent time.

**Neogyys errans* Miller. Errant eagle

17 individuals; 173 bones.

**Neophrontops americanus* Miller. American neophron

36 individuals; 549 bones.

These two extinct eaglelike vultures are fairly abundant in the present collection. **Neogyys*, in contrast with the true eagles, is not particularly abundant in fauna 2, and **Neophrontops* is represented by only 46 bones. **Neogyys* is large and stockily built, and resembles *Haliaeetus*. **Neophrontops* is distinctly smaller and resembles *Neophron*, particularly in the weakness of the tarsometatarsus (Miller, 1916; Howard, 1932). **Neophrontops* must have nested in the vicinity of the asphalt deposits, since bones of immature individuals are present in the C.I.T. collection.

Accipiter striatus velox (Wilson). Sharp-shinned hawk

2 individuals; 14 bones.

Accipiter cooperii (Bonaparte). Cooper's hawk

14 individuals; 108 bones.

The sharp-shinned hawk has not been previously found at McKittrick, and the Cooper's hawk is represented by only two bones. These birds usually hunt in thickets or forested regions, and they were probably present only in small numbers in the open country near the tar seeps.

Buteo jamaicensis (Gmelin). Red-tailed hawk

32 individuals; 391 bones.

Buteo swainsoni Bonaparte. Swainson's hawk

31 individuals; 297 bones.

Buteo regalis (Gray). Ferruginous roughleg

25 individuals; 277 bones.

The collection from McKittrick locality 2 contains 80 bones of the red-tailed hawk, 53 bones of Swainson's hawk, and 26 bones which were not assigned to species. The bones of these hawks are generally distinguishable only by size and proportion of parts. Since there is an overlapping in size among the three species, it is quite probable that specific identification based on the dissociated bones of these birds has been confused to some extent.

*Hypomorphnus *fragilis* (Miller). Fragile eagle

52 individuals; 596 bones.

This small, slender-limbed eagle resembles the buteonid hawks. The tarso-metatarsus is of about the same length as that in *Geranoaëtus melanoleucus*, but the width is much less (Miller, 1911; Howard, 1932).

*Spizaëtus *grinnelli* (Miller). Grinnell's eagle

4 individuals; 6 bones.

Spizaëtus has not been previously reported from the McKittrick asphalt. According to the original description, it "resembles *Geranoaëtus melanoleucus* in general, but is slightly more robust and shows superior strength by greater production of the hypotarsal ridge and lower position of the papilla of the tibialis anticus" (Miller, 1911).

Aquila chrysaëtos (Linnaeus). Golden eagle

126 individuals; 1810 bones.

This is by far the most abundant species in the fossil collections previously described from McKittrick and Rancho La Brea. In the present collection, it is the most abundant in total number of bones and fragments, but not in the minimum number of individuals. In this respect it is surpassed by the burrowing owl and the sparrow hawk.

Haliaeetus leucocephalus (Linnaeus). Bald eagle

14 individuals; 128 bones.

Bones of this eagle are not very numerous in the collection, probably because the bird prefers to live near the coast. The species was not listed in the two collections described by Miller (1925, 1935). It was first recorded from this locality by Howard in 1932.

Circus hudsonius (Linnaeus). Marsh hawk

53 individuals; 607 bones.

This marsh-dwelling hawk was represented in fauna 1 by half a dozen specimens of characteristic parts, and in fauna 2 by 63 bones. In the present collection there is a wide variation in size of the bones, probably due to a difference in sex.

*Polyborus *prelutosus prelutosus* Howard. Rancho La Brea caracara

16 individuals; 158 bones.

Four specimens of this aberrant hawk (listed originally as *Polyborus cheriway*) were found in fauna 1, and 30 in fauna 2. In 1938 Dr. Howard assigned the caracara bones from Rancho La Brea to the new species *P. *prelutosus*, and referred the material from McKittrick to this type. With the description of a new subspecies of caracara from Mexico (Howard, 1940), the California bird becomes *P. *p. prelutosus*.

Falco mexicanus Schlegel. Prairie falcon

70 individuals; 839 bones.

*Falco *swarthi* Miller. Swarth's falcon

2 individuals; 9 bones.

Falco peregrinus Tunstall. Duck hawk

17 individuals; 132 bones.

Falco columbarius Linnaeus. Pigeon hawk

12 individuals; 81 bones.

Falco sparverius Linnaeus. Sparrow hawk.

131 individuals; 1397 bones.

Many of the falcons inhabit open fields and deserts, where they hunt for small vertebrates and insects. They probably were attracted to the tar seeps by the presence of these small animals. The prairie falcon is represented in fauna 2 by 65 bones, Swarth's falcon by 4, the duck hawk by 15, the pigeon hawk by 10, and the sparrow hawk by 102 specimens. The last species was second in number only to the golden eagle in McKittrick fauna 1, and is second also in the California Institute collection. Bones of a few immature sparrow hawks are included in the fossil accumulation. Certain elements of the skeletons of *Falco mexicanus* and *F. peregrinus* are not readily distinguishable except by size, and as there is no break in the series where one may draw the line, some of these bones may not be correctly classified. *Falco *swarthi*

resembles *F. mexicanus* closely, but exceeds it in size and differs from it in a few other characters (Miller, 1927).

Unidentified Falconiformes

More than 170 bones of hawks and eagles are not identified as to genus and species. Most of these probably belong to species identified on the basis of more diagnostic skeletal elements.

GALLIFORMES (Fowl-like Birds)

The California quail is apparently the only species of gallinaceous bird occurring in this deposit. The extinct turkey, **Parapavo californicus*, so abundant at Rancho La Brea, is still not recorded from the McKittrick region.

Lophortyx californica (Shaw). California quail

88 individuals; 762 bones.

Only 3 bones of the California quail occur in fauna 1, and 92 in fauna 2. No other galliform is present. In the present collection, the quail bones vary widely, grading up in size from that of a small California quail to that of the plumed quail (*Oreortyx picta*). The specimens are here grouped together, however, as one variable species. These birds are gregarious ground dwellers on the chaparral-covered hillsides of the Upper Sonoran zone (Hoffmann, 1927).

GRUIFORMES (Cranelike Birds)

Minimum number of individuals, 17.

Total number of bones and fragments, 224.

Cranes are often found near small ponds on sagebrush-covered plains, and now winter in the flat country in the vicinity of McKittrick (Hoffmann, 1927; Miller, 1935).

Grus americana (Linnaeus) (?). Whooping crane

1 individual; 1 bone.

Grus canadensis (Linnaeus). Little brown crane

11 individuals; 158 bones.

Grus, sp. (?). Crane

5 individuals; 65 bones.

The whooping crane has not been previously listed from McKittrick, and is here recorded tentatively because of lack of comparative material. The little brown crane was present in previous collections, 86 bones occurring in fauna 2. In 1925, Miller stated that the bones of this crane are intermediate in size between those of the living *Grus canadensis* and *G. mexicanus*. This is true also of the material in the California Institute collection. The bones which are unidentified specifically are variable in size, but are generally larger than the comparable elements of *G. mexicanus* available in the osteological col-

lection of Dr. Miller. It does not seem advisable to make definite specific determination until more comparative material is available. One grüne skull, almost complete, is of particular interest. It is about as long as that of *G. canadensis*, but the bill is much heavier. The cranium is worn away on one side, but is noticeably smaller than in the modern birds with which it was compared.

CHARADRIIFORMES (Ploverlike Birds)

Minimum number of individuals, 270.

Total identified bones and fragments, 995.

These birds are usually found on the muddy borders of sloughs, marshes, and bays, or on the beach. The killdeer and mountain plover, however, also frequent flat open country and broad valleys (Hoffmann, 1927).

Eupoda montana (Townsend). Mountain plover

31 individuals; 132 bones.

Oxyechus vociferus (Linnaeus). Killdeer

88 individuals; 462 bones.

Unidentified plover

3 individuals; 7 bones.

The mountain plover is represented in fauna 2 by 74 bones. The killdeer was not listed by Miller in 1935, and is but poorly represented in fauna 1. Both birds are fairly abundant in the present collection, and probably nested in the region, as is indicated by the presence of bones of young individuals.

Totanus melanoleucus (Gmelin). Greater yellowlegs

40 individuals; 191 bones.

Numenius americanus Bechstein. Long-billed curlew

1 individual; 2 bones.

Phaeopus hudsonicus (Latham). Hudsonian curlew

3 individuals; 8 bones.

Pelidna alpina (Linnaeus) (?). Red-backed sandpiper

3 individuals; 4 bones.

Limnodromus griseus (Gmelin). Dowitcher

17 individuals; 102 bones.

The greater yellowlegs is represented in fauna 2 by 37 bones, and the long-billed curlew by 2 bones. The Hudsonian curlew has not been found at McKittrick before, and the red-backed sandpiper and dowitcher do not occur in fauna 2. The greater yellowlegs and the dowitcher apparently nested in the region.

Recurvirostra americana Gmelin. Avocet

10 individuals; 94 bones.

This was the most abundant shore bird in fauna 1, and is represented by 37 bones in fauna 2.

Unidentified Charadriiformes

More than 275 bones of shore birds still remain to be identified. They represent at least 74 individuals.

COLUMBIFORMES (Pigeonlike Birds)

This order is represented in the asphalt only by the mourning dove, a species which lives in open fields and ranges, but roosts in trees at night. It rarely alights in marshy places, and was probably attracted to the small pools of drinking water found in the vicinity (Hoffmann, 1927; Miller, 1925, 1935).

Zenaidura macroura (Linnaeus). Mourning dove

44 individuals; 172 bones.

Sixteen bones of this species are found in fauna 2. Bones of immature doves occur in the present collection.

CUCULIFORMES (Cuckoolike Birds)

The road runner is the only cuculine present in the collection. Like the quail and doves, this bird is an indicator of low brush in the near vicinity of the tar seeps, and, like them, it probably came to the region to drink even though the marshy ground was not to its liking.

Geococcyx californianus (Lesson). Road runner

31 individuals; 229 bones.

Only one specimen of this species occurs in McKittrick fauna 1, but it is well represented in fauna 2. Numerous incompletely ossified bones of immature road runners are found in the present collection.

STRIGIFORMES (Owls)

Minimum number of individuals, 282.

Total number of bones and fragments, 3019.

Most of these nocturnal predators live in or near wooded regions, but the short-eared owl prefers marshy or open country in the lowlands, and the very abundant burrowing owl lives in burrows in barren fields. The latter species seems to be independent of a natural water supply, but was probably attracted to the area by insects and small vertebrates caught in the asphalt.

Tyto alba (Scopoli). Barn owl

30 individuals; 273 bones.

The barn owl has not been previously recorded from McKittrick, but is fairly abundant in the C.I.T. collection. These birds live in valleys and foothills, but are not common in heavily wooded regions.

Bubo virginianus (Gmelin). Great horned owl

9 individuals; 81 bones.

Speotyto cunicularia (Molina). Burrowing owl

166 individuals; 1738 bones.

Asio wilsonianus (Lesson). Long-eared owl

31 individuals; 339 bones.

Asio flammeus (Pontoppidan). Short-eared owl

46 individuals; 588 bones.

Twelve bones of the versatile great horned owl were found at locality 2. In the present collection, many of the bones of this species are large, falling just within the range of variability of the owls at Rancho La Brea (Husband, 1924). The burrowing owl, represented by only 26 bones in fauna 2, is the most abundant species in the C.I.T. collection, in number of individuals present. It apparently nested in the region, for bones of young birds occur in the assemblage. The long-eared owl prefers to live in wooded regions but also occurs in the desert. Twenty-one bones of this species occur in fauna 2. The short-eared owl, a dweller in marshy country, has not been previously found in the McKittrick asphalt, but is rather abundant in the present collection. There is an intergradation in the size of some elements of the skeleton between this species and the long-eared owl. It is possible, therefore, that some of the bones have not been correctly assigned as to species.

CAPRIMULGIFORMES (Goatsuckers, Nighthawks, etc.)

Minimum number of individuals, 4.

Total number of bones and fragments, 10.

The bones referred to this order represent at least two species and furnish the basis for an addition to the list of birds from the Pleistocene or early Recent. These birds are found today on dry, brushy hillsides and open deserts in southern California. It is therefore not surprising to find them living in the San Joaquin Valley region during Pleistocene or early Recent time. According to Lönnberg (1927), birds of this order appear to have originated in South America, and to have entered North America after the southern and northern continental areas were connected in post-Miocene time. It is interesting to note that the cathartiform vultures and the caracara are also presumably of Neotropical origin.

Phalaenoptilus nuttalli (Audubon) (?). Poorwill

2 individuals; 4 bones.

Chordeiles acutipennis Lawrence (?). Texas nighthawk

1 individual; 3 bones.

Chordeiles, sp. (?). Nighthawk

1 individual; 3 bones.

The bones of these birds appear to differ slightly from comparable ele-

ments in Recent skeletons in the collections of the University of California at Los Angeles and of the Los Angeles Museum. It does not seem advisable, therefore, to give them positive specific identification until additional comparative material becomes available.

PICIFORMES (Woodpeckers, etc.)

The woodpeckers are represented by the aberrant flicker and a smaller species which has not yet been identified. In previous McKittrick collections, the flicker is the only woodpecker recorded.

Colaptes cafer (Gmelin). Red-shafted flicker

5 individuals; 19 bones.

Eight bones of this species are found in fauna 2. It is rather surprising that relatively few individuals are known, since this ground-dwelling bird might be expected to occur in larger numbers.

Unidentified Piciformes

Five pelves are assigned to this order, but have not been identified as to species. They are not included in the census.

PASSERIFORMES (Sparrowlike Birds)

Minimum number of individuals, 505.

Estimated total number of bones, about 4000.

Although hundreds of bones of small passerines occur in the collection, most of these still need to be classified. Bones of the raven, however, are more readily identified, and their number is included here. A. H. Miller (1937) states that the crow is absent from the McKittrick passerine materials available to him for study. In the present collection, however, there are several passerine bones which fall within the size range of modern crows.

Passerines recorded from McKittrick by A. H. Miller (1937) include the Bendire thrasher (*Toxostoma bendirei*), cliff swallow (*Petrochelidon albifrons*), house finch (*Carpodacus mexicanus*), cactus wren (*Heleodytes* sp.), and sage sparrow (*Amphispiza belli*). These are not found at Rancho La Brea or at Carpinteria. In addition, Dr. A. H. Miller has found the following species in the McKittrick fauna: horned lark (*Otocoris alpestris*), sage thrasher (*Oreoscoptes montanus*), loggerhead shrike (*Lanius ludovicianus*), California jay (*Aphelocoma californica*), magpie (*Pica*), raven (*Corvus corax*), white-necked raven (*Corvus cryptoleucus*), and meadowlark (*Sturnella neglecta*).

Petrochelidon albifrons (Rafinesque). Cliff swallow

No attempt is made to identify all the skeletal parts of this swallow. The humerus, which has a characteristic shape, does occur in the collection, however. These mud-gatherers are represented in the earlier McKittrick collection.

Corvus corax Linnaeus. Raven

46 individuals; 582 bones.

Very few bones of ravens were found in fauna 1, but 110 bones of the genus *Corvus* are reported from fauna 2. Young individuals of this variable passerine occur in the present collection.

Unidentified passerines

458 individuals.

At the suggestion of Dr. A. H. Miller, a count was made of all humeri of passerines in the present collection, and the total for the side most numerous-ly represented (right or left) was taken to indicate the minimum number of individuals present. In making this count, the humerus was chosen because it is one of the most characteristic elements, and is sufficiently well preserved in the fossil avifauna to make possible a fairly accurate estimate of the number of birds present. The exact number of bones has not been determined, but an estimate based on the number of individuals places the total at about 4000.

SPECIES NOT RECORDED

Species previously found at McKittrick which do not appear in the avifauna from locality 138 are as follows: whistling swan (*Cygnus columbianus*), one bone from fauna 2; Dickey's goose (*Branta *dickeyi*), one bone from fauna 1; snow goose (*Chen hyperborea*), two bones, fauna 1; ruddy duck (*Erismatura jamaicensis*), two or three bones, both faunas; and Virginia rail (*Rallus limicola*), two bones, fauna 1 (L. H. Miller, 1924, 1925, 1935). It is suggested that the great scarcity of the anserines listed above may be due to the shallowness of the water in the vicinity of the asphalt seeps when the McKittrick fauna accumulated.

ECOLOGIC RELATIONSHIPS OF AVIFAUNA

Previous investigations of the McKittrick avifauna in the collections of the University of California have demonstrated that two-thirds of the species from fauna 1 are aquatic or semiaquatic in habit, and that only one-fourth of the species from fauna 2 belong to this ecologic group. In the present collection also, one-fourth of the individuals are aquatic or semiaquatic and three-fourths are terrestrial. The accompanying diagram (fig. 1) shows

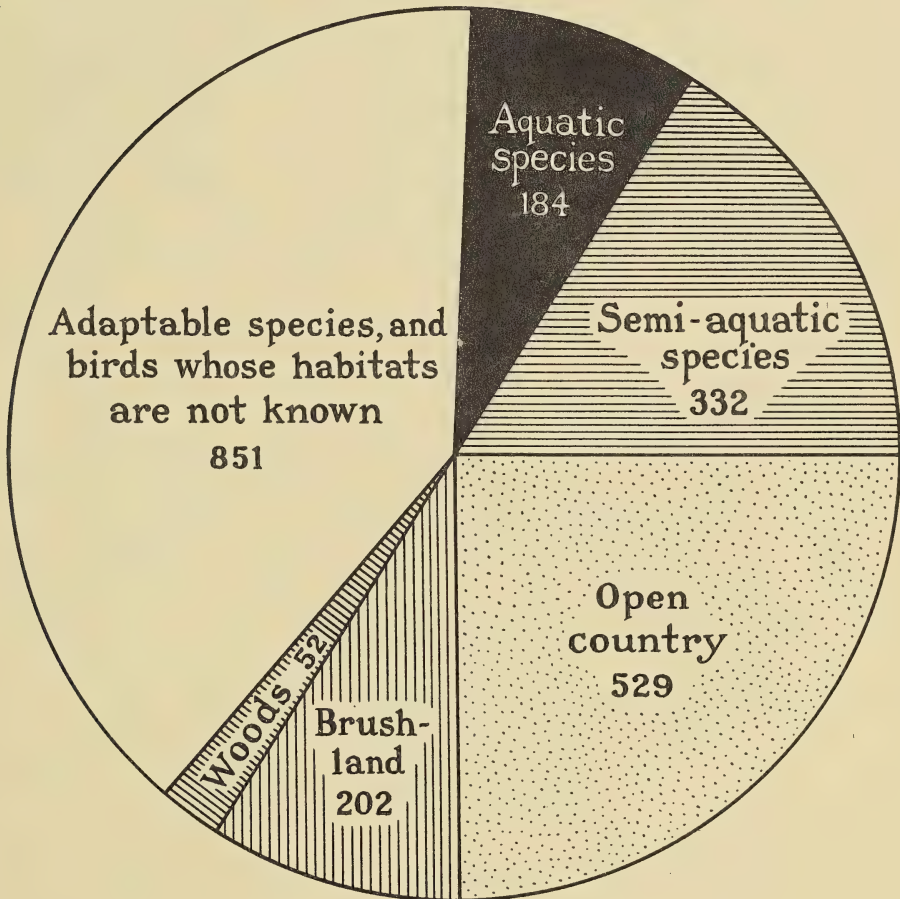


Fig. 1

the relative significance of the several ecologic niches occupied by the birds that occur in the asphalt. The sectors representing the relative importance of open country and chaparral in and about the McKittrick tar seeps during their active period are based upon the number of nonaquatic species

that in large measure inhabit these environments. The size of these segments in the diagram will doubtless increase greatly when all the small passerines in the collection are identified.

The Falconiformes in the C.I.T. collection do not form proportionately so large a group as at Rancho La Brea (see fig. 2), but the percentage of owls



Fig. 2

in the McKittrick collection is about twice as great as that at Rancho La Brea. The number of Galliformes at the Los Angeles locality is striking because of the great numerical representation of the extinct turkey, **Parapavo*. This species has not been found at McKittrick, and the gallinaceous birds occupy only a small place in the fauna (see fig. 2).

The number of individuals for each species of which 10 or more individuals are present in the avifauna from locality 138 is recorded in figure 3. The

burrowing owl, with at least 166 individuals present, is the most abundant species in the collection. The sparrow hawk is second with 131, and the golden eagle third with 126. It is interesting to note that bones of the golden eagle are most abundant in McKittrick fauna 2, with the fragile eagle second

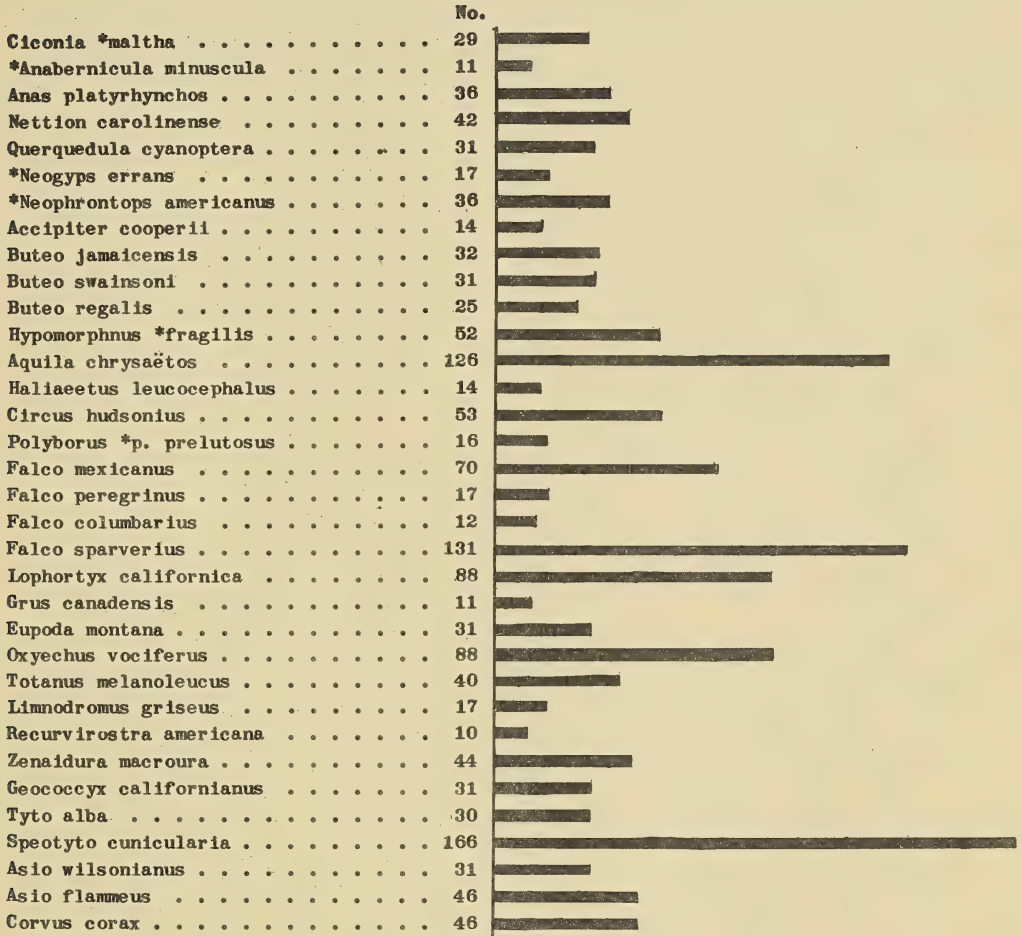


Fig. 3. Number of individuals in each species of bird (excluding small passerines) represented by ten or more individuals at McKittrick locality 138.

and **Teratornis* third. The sparrow hawk is fairly abundant in the latter collection, but the burrowing owl is represented by only 26 bones. According to the census of Rancho La Brea birds made by Howard in 1930, the golden eagle is by far the most abundant species; **Parapavo* is second, and the caracara third. In the Rancho La Brea avifauna, the sparrow hawk is represented by only 12 individuals.

Species new to the McKittrick collections include the following: American egret, some small herons, California condor, sharp-shinned hawk, Grinnell's eagle, a large crane, Hudsonian curlew, barn owl, short-eared owl, a poorwill, and a nighthawk. This is the first fossil record of the Caprimulgiformes.

On the basis of incompletely ossified bones of young individuals occurring in the collection, it is assumed that the following species nested in the McKittrick region: great blue heron, American egret, asphalt stork, sparrow hawk, California quail, mourning dove, road runner, and nighthawk.

FEATURES OF AVIFAUNA DUE TO TIME OF ACCUMULATION

Peculiarities in the mode of accumulation and the type of collecting done at McKittrick make it impossible now to distinguish between the Pleistocene and Recent birds recovered from these deposits. As a matter of fact, the lateness in Pleistocene time of the older fauna and the continuous geologic activity that has occurred in the region, permitting outpours of tar of greater or less size down to the present, increase the difficulty of recognizing faunal differences due to time.

Examination of the skeletal remains of birds leads to the conclusion that the type of preservation of this material was not always the same. As observed in the field, some bones were preserved in clay or sand, others in an almost pure tar. As a consequence there is a difference in the appearance of the specimens. Some are jet black, others brown, and a third group are of still lighter hue. It is not always clear, however, whether a lighter color necessarily results from a shorter period of contact of the bone with petro-liferous substances, and it is thus unsafe to use this criterion in distinguishing between Recent and Pleistocene specimens. As a matter of fact, bones of extinct types of birds may on occasion have a very light color, apparently due to oxidation and bleaching of the material since its entombment. This is especially true of some of the **Parapavo* bones from the Carpinteria asphalt.

Aside from these differences in color, many elements taken from the McKittrick deposits show a toughness and a resistance to stress not seen in others. These qualities may have some geologic age significance and may ultimately be found useful in distinguishing the bones of more recent age from those of the typical Pleistocene. It is significant to note at this point that in the present collection a few bones of small passerines are still attached to each other by ligaments. This type of preservation would seem to indicate that these particular specimens, at least, are Recent in age.

In view of these observations, it is important to keep the factor of time in mind when considering the ecology of the avifauna obtained at locality 138. Thus the smaller percentage of aquatic species in this avifauna, as compared with those previously noted from McKittrick, may indicate that the present collection was made in deposits laid down farther back from the edge of the lake,

or on slightly higher ground. This view seems unlikely, however, since C.I.T. locality 138 and the U.C. locality whence fauna 2 came are in essentially the same area. It is probably more logical to assume that decrease in the number of aquatic birds reflects a change in the environment about the tar seeps as the lake receded in time, with a concomitant increase in representation of Recent forms (see figs. 1, 3).

A number of additional changes should be noted in the composition of the avifauna. In the Institute collection the small predators are very abundant, a marked contrast with Rancho La Brea and McKittrick fauna 2. Burrowing owls and sparrow hawks are present in great numbers, exceeding even the golden eagle in abundance. The large eagles and eaglelike vultures, so characteristic of the typical Pleistocene fauna of Rancho La Brea and McKittrick 2, are not well represented in this collection. It seems probable that much of the avifauna was trapped in the asphalt after most of these large predators became extinct. The fact that the traps were still capable of attracting and mirroring the large flesh-eaters that existed in the region is shown by the presence of great numbers of bones of the golden eagle and smaller numbers of bones of the fragile eagle, marsh hawk, and prairie falcon. It does not seem likely that an environmental barrier was responsible for the scarcity of the larger falconiforms. Several species, as for example the California condor and **Teratornis*, were widely distributed in Pleistocene time, and the eagles and vultures living today are generally not restricted to any one faunal zone.

A comparison of the Recent fauna from pit 10 at Rancho La Brea with that from typical Pleistocene pits of the same locality demonstrates that there has been not only a decrease in the percentage of individuals of extinct species, but also a marked decrease in number of large predators and an increase in number of small ones. In this regard a definite resemblance exists between McKittrick 138 and pit 10 (see fig. 4, p. 58). Judged from its composition, the avifauna from locality 138 falls in time between the Recent and Pleistocene avifaunas of Rancho La Brea. It appears to be definitely younger than the typical Pleistocene fauna of Rancho La Brea and McKittrick 2, but somewhat older than the avifauna from pit 10, Rancho La Brea. Probably the fauna was entombed in successive asphalt flows over a period of several hundred years, beginning in Pleistocene time and continuing into the Recent.

CONCLUSIONS

The great abundance of falcons, buteonid hawks, and small owls in the California Institute collection from McKittrick strongly suggests that there was considerable open country in the region about the tar seeps in late Pleistocene time. The presence of nesting quail, doves, and road runners indicates particularly the presence of chaparral-covered hillsides in the vicinity. The larger owls and the sharp-shinned and Cooper's hawks probably lived in

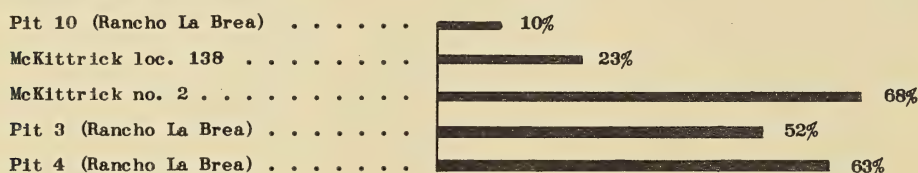
sparsely wooded areas not far from the asphalt traps. The presence of water, mud flats, and marshes near by is certainly indicated by the occurrence of herons, ducks, cranes, shore birds, the marsh hawk, the short-eared owl, and a grebe in the collection.

The absence of the extinct California turkey (**Parapavo californicus*) from McKittrick may be due to lack of sufficient brushy cover in the vicinity or

A. Extinct species:



B. Condors and eagles:



C. Hawks, owls, and falcons:



Fig. 4. Comparison of the avifaunas of Rancho La Brea and McKittrick, showing percentages of (A) individuals of extinct species relative to the total avifauna, excluding Passeriformes, (B) condors and eagles, and (C) hawks, owls, and falcons relative to the total raptorial count. Percentages for Rancho La Brea pits are modified after Howard and Miller (1939).

to the presence of a mountain barrier between the Los Angeles area and the San Joaquin Valley, as suggested by L. H. Miller. Unlike the vultures and eagles, these large gallinaceous birds may have been restricted in habitat. That their absence at McKittrick was controlled by an ecologic rather than by a time factor is suggested by the fact that the species is recorded in the Recent avifauna of pit 10, Rancho La Brea. Also, **Parapavo* is the most abundant species in the Carpinteria avifauna, which appears to be about the same age as McKittrick faunas 1 and 2.

Decrease in number of the larger Falconiformes with noticeable increase in representation of the smaller predatory birds at McKittrick contrasts with the relative abundance of the larger types in the Rancho La Brea Pleistocene,

and is taken to indicate a later stage for the former assemblage. There is, however, reason for believing that some of this lack of antiquity is due to an admixture of a later (Recent, but not present-day) assemblage with a fauna dating from the Pleistocene.

Analysis of the composition of the avifauna from locality 138 leads to the conclusion that the ecologic requisites of most of the birds found in the McKittrick asphalt are satisfied by an environment in which sparsely timbered mountain slopes give way to brush-covered hills and arid or semi-arid plains lying adjacent to a desert lake.

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IV

PLEISTOCENE BIRD LIFE OF THE CARPINTERIA
ASPHALT, CALIFORNIA

IDA S. DeMAY

With four text figures

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PLEISTOCENE BIRD LIFE OF THE CARPINTERIA ASPHALT, CALIFORNIA

INTRODUCTION

Recent studies of the fossil birds in the collection of the California Institute of Technology emphasize the need of a survey of the entire avifauna from the Pleistocene asphalt beds near Carpinteria, California. Material is now available which has not been previously identified or described. Furthermore, the present investigation makes available information regarding the Carpinteria avifauna which permits a fuller and more adequate comparison with the fossil assemblages from Rancho La Brea and McKittrick than has been possible heretofore.

This survey is based on materials from the Carpinteria asphalt in the collections of the California Institute of Technology, the Santa Barbara Museum of Natural History, and the University of California at Los Angeles, and includes the specimens described by L. H. Miller in 1931. The Santa Barbara Museum collection includes small lots of bones collected from time to time by field parties. Some of the specimens were identified by Hildegarde Howard in 1932 and 1934, but no mention of the new material was made in print.

Because the Carpinteria collections were made at various times and by different institutions, it is now difficult to segregate the species into the two avifaunas described by Miller in 1931. As a matter of fact, a separation of this kind appears to serve no particular purpose at the present time. The two original sites of occurrence are now greatly enlarged, and new excavations have been made. For these reasons, the entire avifauna is here considered as a unit.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge my indebtedness to Dr. Chester Stock for the opportunity to study the Carpinteria collection at the California Institute of Technology and for his helpful suggestions and encouragement. Thanks are likewise extended to Dr. Loye Miller, who has made available the Carpinteria material at the University of California at Los Angeles, as well as his comparative collection of Recent bird skeletons.

I am indebted to Dr. Hildegarde Howard for her constructive criticism and many helpful suggestions in the preparation of this paper. Dr. Howard not only has permitted use of bird material in the Rancho La Brea and Recent collections of the Los Angeles Museum, but has helped in the identification of a number of specimens. Phil C. Orr, of the Santa Barbara Museum of Natural History, permitted the loan of fossil birds in the Carpinteria collection of the Museum. The diagrams were prepared by David P. Willoughby.

PREVIOUS INVESTIGATIONS

Bones of mammals and birds, as well as plant remains, were first discovered in the Pleistocene asphalt near Carpinteria in February 1927, and a preliminary

notice (Hoffmann, Stock, and others, 1927) of this fossil find was published in that same year. Since then, a number of papers have appeared in which attention has been directed to particular groups of organisms, namely, the mammals, birds, plants, or invertebrates. These reports have contributed important facts relating to the environmental conditions that prevailed at the time of accumulation and to the age relationships of the faunas and floras.

Thus, the fossil birds were discussed by Loye Miller in 1931, and the passerine group was reported upon by A. H. Miller in the following year. Howard (1938) determined the specific status of the caracara. The rich and well preserved flora was discussed in detail by Chaney and Mason (1934). In this paper appeared also a chapter by Irma E. Webber on the wood preserved in the deposit. R. W. Wilson (1933) reported on the Pleistocene mammalian fauna. Lastly, U. S. Grant and A. M. Strong (1934) made a study of the marine molluscan fauna preserved in the tar sands which contain the plant and vertebrate fossils.

DISCUSSION OF SPECIES

As in the preceding paper on the avifauna from the McKittrick asphalt (De-May, 1941), the arrangement of species follows that of the *Check-list of the fossil birds of North America* (Wetmore, 1940). The method employed in determining the number of individuals in each species is likewise the same as that previously described.

At least 351 individual birds, including unidentified small passerines, are recorded by the present census. Thus far, more than 2400 bones and bone fragments have been identified in the Carpinteria collections. In addition, a number of bones still remain unidentified. Most of these belong to small passerines.

PELECANIFORMES (Pelicans and Their Allies)

Pelecanus occidentalis Linnaeus. Brown pelican

1 individual; 1 bone.

One of the interesting discoveries resulting from the present survey of the Carpinteria avifauna rests in the recognition of a left scapula of the brown pelican. This species was not previously recorded as a fossil, and is the first pelican to be found in the fossiliferous asphalt deposits of California (see Wetmore, 1940). Its presence in the Carpinteria collection is noteworthy, because it represents the first definitely identified marine bird found in this forest- and bush-dwelling fauna.

CICONIIFORMES (Storklike Birds)

*Ciconia *maltha*¹ Miller. Asphalt stork

6 individuals; 22 bones.

¹An asterisk (*) before a name indicates that the genus or species is extinct.

A stream or small pond near the asphalt traps may have offered congenial surroundings to the small number of storks caught in the tar. These birds probably nested somewhere in the vicinity, if we may judge from the presence of incompletely ossified bones in the fossil assemblages.

ANSERIFORMES (Gooselike Birds)

Chen (?) sp. Goose

1 individual; 1 bone.

Anas platyrhynchos Linnaeus. Mallard

1 individual; 7 bones.

Ducks and geese are poorly represented in the deposit. A single fragment of a tarsus was tentatively referred to the genus *Chen* by Miller in 1931. In this paper, Miller also makes note of the fact that the mallard duck shows considerable adaptability. Consequently, the bird has little value as an indicator of type of habitat.

FALCONIFORMES (Falconlike Birds)

Minimum number of individuals, 125.

Total number of identified bones and fragments, 1427.

Cathartes aura (Linnaeus). Turkey vulture

3 individuals; 22 bones.

Coragyps occidentalis (Miller). Western black vulture

4 individuals; 13 bones.

Gymnogyps californianus (Shaw). California condor

3 individuals; 15 bones.

**Teratornis merriami* Miller. Merriam's teratorn

4 individuals; 21 bones.

**Neogyps errans* Miller. Errant eagle

10 individuals; 188 bones.

**Neophrontops americanus* Miller. American neophron

2 individuals; 13 bones.

With the exception of **Neogyps*, none of these cathartiform and eaglelike vultures is well represented in the collection. Miller (1931) believes that the scarcity of birds of the open country, for example the vultures, lends support to the view that the region was forested. The ratio of *Cathartes* to *Coragyps*, which is more than two to one at McKittrick and about one to five at Rancho La Brea, is approximately one to one in the Carpinteria avifauna. The ratio appears to be a reliable index of antiquity of the Quaternary avifaunas in which these genera occur. Its value in the instance of Carpinteria, however, seems to be lessened somewhat by the fact that the environment at the latter locality was not attractive to these birds. The reasons for a much greater representation of **Neogyps* than of *Aquila* are not immediately apparent.

Astur atricapillus (Wilson). Goshawk

4 individuals; 10 bones.

Accipiter striatus velox (Wilson). Sharp-shinned hawk

1 individual; 2 bones.

Accipiter cooperii (Bonaparte). Cooper's hawk

8 individuals; 83 bones.

Buteo jamaicensis (Gmelin). Red-tailed hawk

20 individuals; 350 bones.

Buteo lineatus (Gmelin). Red-shouldered hawk

7 individuals; 76 bones.

Buteo regalis (Gray). Ferruginous roughleg

8 individuals; 84 bones.

The goshawk, sharp-shinned hawk, and Cooper's hawk are inhabitants of forest or brushland, and their presence here substantiates the belief that the region was wooded. The buteonid hawks are found not only in forested or brushy areas, but also in open country. This is especially true of the versatile red-tailed hawk.

*Hypomorphnus *fragilis* (Miller). Fragile eagle

6 individuals; 103 bones.

**Wetmoregyps daggetti* (Miller). Daggett's eagle

3 individuals; 38 bones.

*Spizaetus *grinnelli* (Miller). Grinnell's eagle

8 individuals; 82 bones.

Aquila chrysaetos (Linnaeus). Golden eagle

7 individuals; 108 bones.

Haliaeetus leucocephalus (Linnaeus). Bald eagle

5 individuals; 59 bones.

In a region presumably not far removed from the strand line one might expect to find the bald eagle in greater numbers than is actually the case in these collections. The golden eagle is not well represented either. By comparison, these birds occur in great abundance at Rancho La Brea and McKittrick. Their relative scarcity at Carpinteria may be due to climatic conditions, since golden eagles are not common today in the humid coastal belt of California (Hoffmann, 1927). Habitat preferences of the extinct eagles, of course, can only be surmised.

Circus hudsonius (Linnaeus) (?). Marsh hawk

1 individual; 1 bone.

A single humerus was tentatively assigned to this species by Miller (1931). According to Dr. Miller, the scarcity of this bird at Carpinteria is to be expected.

*Polyborus *prelutosus prelutosus* Howard. Rancho La Brea caracara

7 individuals; 76 bones.

Falco sparverius Linnaeus. Sparrow hawk

14 individuals; 83 bones.

The caracara, formerly identified as *P. cheriway*, was recognized as a new species, *P. *prelutosus*, by Howard in 1938. With the description of a new subspecies from Mexico, the California bird becomes *P. *p. prelutosus* (Howard, 1940). The species is relatively less abundant here than at Rancho La Brea. The sparrow hawk, surprisingly enough, is the only falcon found in the Carpinteria asphalt. It is usually a hunter of the open fields, never dashing through thickets and the foliage of trees like the pigeon hawk (*F. columbarius*) or sharp-shinned hawk, according to Hoffmann (1927). The duck hawk (*F. peregrinus*) lives today along the rocky coast of California, but is not found in the Carpinteria asphalt. The sparrow hawk apparently nested in the region, for bones of young birds are present in the collection.

Unidentified Falconiformes

A number of bones in the collection remain unidentified. These are not included in the census.

GALLIFORMES (Fowl-like Birds)

Lophortyx californica (Shaw). California quail

9 individuals; 102 bones.

**Parapavo californicus* (Miller). California turkey

37 individuals; 481 bones.

**Parapavo* is by far the most abundant species found in the collection, and *Lophortyx* is fairly well represented. Both species apparently nested in the region. As previously noted, the turkey is extremely abundant at Rancho La Brea, but is absent at McKittrick. These birds presumably inhabited brushy or wooded regions, and this type of environment doubtless contrasted sharply with the more open terrain of southwestern San Joaquin Valley. Bones of quail, which are very numerous at McKittrick, are quite scarce at Rancho La Brea.

CHARADRIIFORMES (Ploverlike Birds)

Minimum number of individuals, 2.

Total number of bones and fragments, 2.

A fragment of a tarsometatarsus in the Santa Barbara Museum collection has previously been identified as that of a shore bird. The specimen is so fragmentary that no further identification has been attempted. An ulna resembling the corresponding bone of the mountain plover (*Eupoda montana*), but differing in several details, has been found in the collections of the California Institute of Technology. These two bones are the only specimens representing this order which have thus far been recognized in the Carpinteria avifauna.

COLUMBIFORMES (Pigeonlike Birds)

Columba fasciata Say. Band-tailed pigeon

1 individual; 4 bones.

Zenaidura macroura (Linnaeus). Mourning dove

1 individual; 1 bone.

Miller (1931) commented on the fact that these birds are scarce in both the Carpinteria and Rancho La Brea collections, although they are now abundant in California. The mourning dove is represented by a single bone in the Carpinteria collection, but is fairly common at McKittrick. The band-tailed pigeon, a forest-dwelling species, does not occur at all in the McKittrick asphalt.

CUCULIFORMES (Cuckoolike Birds)

Geococcyx californianus (Lesson). Road runner

11 individuals; 80 bones.

This species is found today in deserts and brush-covered foothills throughout southern California (Hoffmann, 1927). It is fairly well represented by adult and immature specimens in all three asphalt deposits.

STRIGIFORMES (Owls)

Minimum number of individuals, 23.

Total number of bones and fragments, 242.

Tyto alba (Scopoli). Barn owl

1 individual; 3 bones.

Otus asio (Linnaeus). Screech owl

3 individuals; 29 bones.

Bubo virginianus (Gmelin). Great horned owl

11 individuals; 172 bones.

Glaucidium gnoma Wagler. Pygmy owl

5 individuals; 23 bones.

Asio wilsonianus (Lesson). Long-eared owl

3 individuals; 15 bones.

It has previously been suggested (Miller, 1931) that the scarcity of barn owls at Carpinteria is due to their dislike of heavily forested regions. The versatile screech owls and great horned owls are of little value as indicators of type of habitat, but the pygmy and long-eared owls prefer wooded regions in the mountains and along the coast. The desert-dwelling burrowing owl, so numerous in the McKittrick assemblage, remains entirely absent at Carpinteria. Bones of immature screech owls are present in the collection.

PICIFORMES (Woodpeckers, etc.)

Minimum number of individuals, 25.

Total number of identified bones and fragments, 101.

Colaptes cafer (Gmelin). Red-shafted flicker

12 individuals; 70 bones.

Asyndesmus lewis (Gray). Lewis's woodpecker

3 individuals; 25 bones.

Dryobates, sp. (?). Woodpecker

3 individuals; 6 bones.

Unidentified woodpeckers

7 individuals; 20 bones.

Specific assignment of the smaller woodpeckers does not seem justified until further study of these specimens is made. Miller (1931) lists "a woodpecker about the size of *Dryobates vilosus*," and states that "all members of the genus are more sylvan in habitat than is the flicker."

PASSERIFORMES (Sparrowlike Birds)

Estimated number of individuals, 108.

The passerines from Carpinteria were described by A. H. Miller in 1932 and 1937. Since only a partial census was given in these papers, a count was made of the passerine bones identified by Miller which are now at the Santa Barbara Museum. Additional material mentioned in Miller's publications and in a notation found at the Museum has been included in the total, together with 54 individuals in collections of the Santa Barbara Museum and California Institute of Technology, which have not been examined by Dr. Miller. Seven of these are ravens, 4 are crows, and 43 are unidentified small passerines. The last figure was determined by counting either the left or right humeri in the collections at hand.

The following species of perching birds have been found in the Carpinteria asphalt:

Sayornis, sp. (?). Phoebe

Empidonax, sp. (?). Small flycatcher

Indeterminate flycatcher

Cyanocitta stelleris (Gmelin). Steller's jay

Aphelocoma californica (Vigors). California jay

Pica nuttalli (Audubon). Yellow-billed magpie

Corvus corax Linnaeus. Raven

Corvus caurinus Baird. Northwestern crow

Penthestes, sp. (?). Chickadee

Sitta canadensis Linnaeus. Red-breasted nuthatch

Sitta pygmaea Vigors. Pygmy nuthatch

Chamaea fasciata (Gambel). Wren tit

Turdus migratorius Linnaeus. Robin

Hylocichla (?). Thrush

Sialia mexicana Swainson. Mexican bluebird

Bombycilla cedrorum Vieillot. Cedar waxwing
Sturnella neglecta Audubon. Western meadowlark
Spinus pinus (Wilson). Pine siskin
Loxia curvirostra Linnaeus. Red crossbill
Pipilo maculatus Swainson. Spotted towhee
Pipilo fuscus Swainson. Brown towhee
Passerella iliaca (Merrem). Fox sparrow
Indeterminate fringillids, etc.

ECOLOGIC FEATURES OF AVIFAUNA

Previous studies of the remains of animals and plants from the Carpinteria asphalt have shown that many species are the same as those now found in the fog belt near the Monterey peninsula. This is particularly true of plants and small animals that are restricted in habitat. A comparison of this Pleistocene fauna with the Recent fauna described by Grinnell and Linsdale (1936) from Point Lobos Reserve, an area of about 330 acres in Monterey County, may therefore reveal some points of special interest.

Grinnell and Linsdale found 147 species of birds living in the Point Lobos area. Of these, 28 per cent owe their presence directly to the influence of the ocean. This is in marked contrast to the Carpinteria fauna, in which only 3 per cent of the species are aquatic or semiaquatic in habit (see fig. 1). In this respect, the Carpinteria avifauna greatly resembles that of Rancho La Brea and differs from that of McKittrick, where about 25 per cent of the birds belong to species that now live near lakes and bays.

Of the terrestrial species at Point Lobos, nearly half were found to be birds which forage mainly or entirely on the ground, and one-fourth to be kinds which usually hunt for food on the bare trunks or dead limbs of trees. Analysis of the figures presented in the Carpinteria census shows that approximately one-fifth of the birds forage mainly on the ground and one-tenth on trunks and limbs of trees. The ratio of these groups is about two to one in both faunas. It is important to note that only one-tenth of the land birds at Point Lobos are carnivorous, whereas nearly half of those at Carpinteria are predators. Obviously the Pleistocene fauna is not a balanced assemblage. Such a large proportion of carnivorous species could not possibly exist under natural conditions, where many small birds and mammals are necessary to support a single hawk or owl, but in the asphalt traps a single quail might very well cause the death of many predators.

According to Grinnell and Linsdale, the environmental conditions in the Point Lobos Reserve can be readily segregated into four distinct habitat groups: grassland, brushland, forest, and ocean shore. Some evidence of the presence of each of these is seen also at Carpinteria. Grasses and low shrubs cover nearly half the ground surface of the Reserve, but open fields in the vicinity of the Carpinteria asphalt trap probably were not extensive. Less than one-

sixth of the species which have known habitat preferences are birds of the open country (see fig. 1). Although the brushland and forest at Point Lobos Reserve occupy less surface area than the grassland, they constitute important parts of the environment because they provide a variety of ecologic niches and greatly increase the habitable space above the ground. Lupine, poison oak, and *Ceanothus* are predominant in the brushland, and live oaks, cypresses, and Monterey pines are the only trees represented in sufficient numbers to exert much influence on the vertebrate animals living in the area. In the

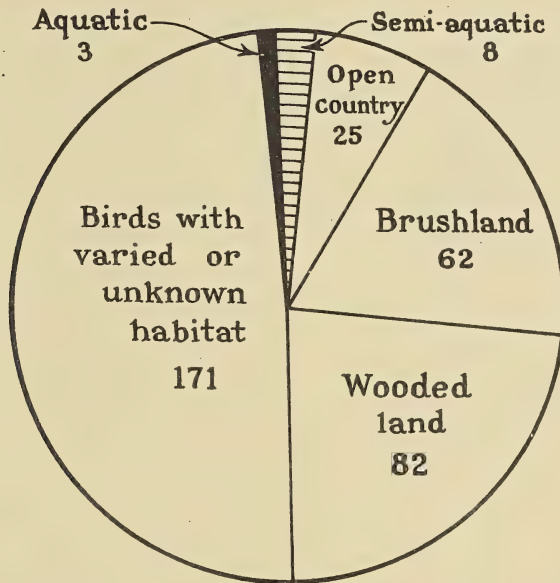


Fig. 1. Relative importance of the ecologic niches occupied by the birds from the Carpinteria asphalt.

Carpinteria asphalt, conifers make up by far the larger part of the collection of plant remains, with an abundance of cones, needles, and wood. Approximately one-half of the land birds found in the asphalt are kinds which now live in wooded regions, and more than a third are inhabitants of the chaparral. When more passerines have been identified, the percentage of forest dwellers will probably be greatly increased. Apparently, then, the Pleistocene tar deposit at Carpinteria was situated in a region similar to the Point Lobos area, but more heavily wooded.

The scarcity of aquatic species in the Carpinteria avifauna suggests that during Pleistocene time the asphalt lens was more remote from the sea cliff than is the case at present, and that no large body of fresh water like the Pleistocene lake at McKittrick existed in the vicinity. It is interesting to note, however, that a single bone of the brown pelican is present in the Carpinteria collection. This species happens to be of special interest at Point Lobos, also, because it is easily recognized and occurs in large numbers in a breeding colony on Bird Island.

It should be remembered that in making a survey of the Point Lobos fauna the observer moves from place to place and includes in his list not only the

birds that are actually found in the area but also those that fly overhead or that are seen offshore. It is impossible, of course, to make such a survey of a fossil avifauna. The paleontologist must confine his observations to the species which have actually left their remains in a deposit. Certain birds like the Brandt and pelagic cormorants, western gull, bush tit, linnet, and white-crowned sparrow are important members of the avifauna at Point Lobos, but they are not known to occur in the Carpinteria collections. The marine species may have been present along the shore near Carpinteria in Pleistocene time, but apparently these forms were not attracted by the biotic conditions in the immediate vicinity of the asphalt.

Both the road runner and the pygmy nuthatch are of more than ordinary interest at Point Lobos and at Carpinteria. The road runner is characteristically found in the chaparral association; the pygmy nuthatch is almost restricted to the coniferous forests. The presence of both birds in the asphalt and at Point Lobos emphasizes the fact that the two faunas show a transition between the Upper Sonoran and Boreal life zones.

Comparison of the habitat groups of the three asphalt localities indicates that Carpinteria was situated near the edge of a Monterey pine forest in brushy country, with patches of open grassland not far away; Rancho La Brea reflects a chaparral association similar to that of the Los Angeles area today; and the McKittrick asphalt occurred in the Lower Sonoran zone in open or brush-covered country near the lower limits of the Upper Sonoran piñon forest. In numerical representation of birds in each order (see fig. 2) Rancho La Brea tends likewise to occupy an intermediate position. The much greater representation of the Passeriformes in the collections from both Carpinteria and McKittrick is probably due to the special care taken in removing these tiny bones from the matrix. The method of collecting may likewise account, at least in part, for the large number of woodpeckers recovered from the Carpinteria asphalt.

Only two species at Carpinteria are outstanding in point of numbers. These are the California turkey and the red-tailed hawk (see fig. 3). As previously noted, the extinct turkey is entirely absent at McKittrick, but next to the golden eagle it is the most common bird at Rancho La Brea.

AGE RELATIONS

An understanding of the relationships in time of the three California asphalt avifaunas may be obtained from the diagram (fig. 4) showing percentages of extinct species and of large versus small predators. Howard and Miller (1939) found that the Recent or subfossil avifauna from pit 10, Rancho La Brea, differs from a typical Pleistocene avifauna occurring at that locality not only in the marked decrease in extinct species, but also in a decrease in numbers of large condors and eagles and an increase in

representation of the hawks, owls, and falcons. Similar differences are also found when the avifaunas of McKittrick are compared. The percentage of extinct species at Carpinteria is as great as that in a typical Pleistocene avifauna of Rancho La Brea cited by Howard and Miller (1939). The small predators are relatively more abundant and the condors and eagles less abundant

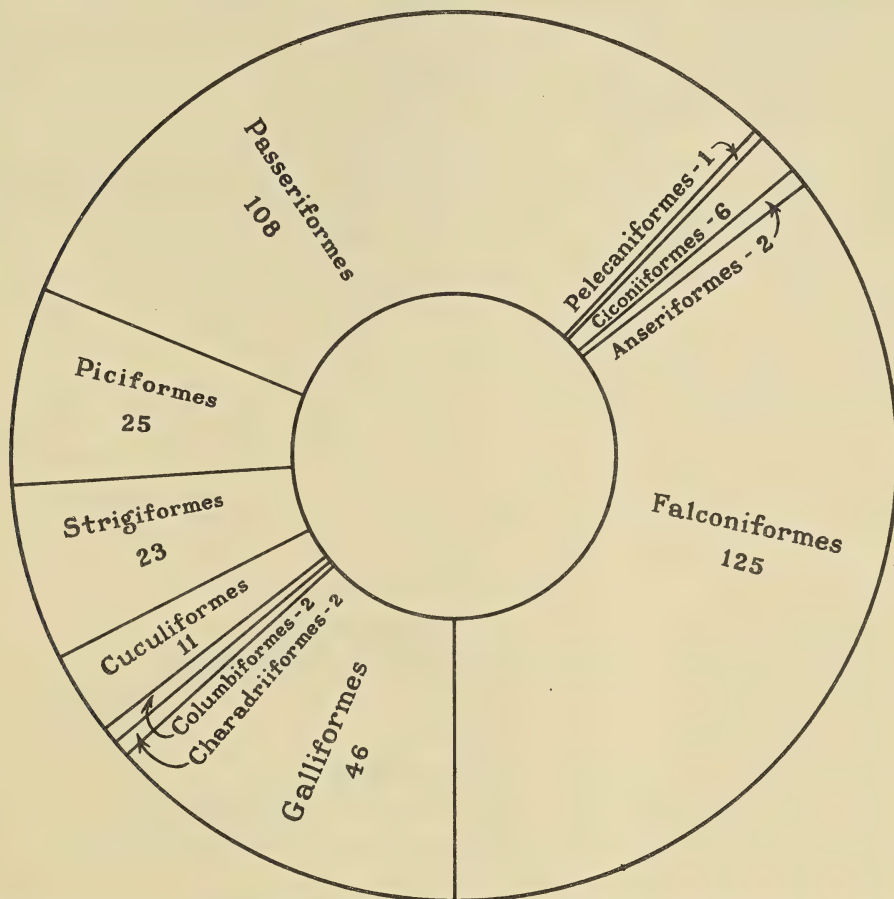


Fig. 2. Relative abundance of individuals in each order of birds occurring in the Carpinteria asphalt.

than in the Pleistocene avifaunas of Rancho La Brea and McKittrick, however. It seems to be a fair assumption that the large condors and eagles, many of which are now extinct, avoided the heavily forested regions in Pleistocene time, exactly as the golden eagle does today. Their scarcity at Carpinteria, then, may be due to a deterring influence of the environment and not to time. It appears probable that the Carpinteria fauna was contemporaneous with that of the Pleistocene of Rancho La Brea, or only slightly younger. The Pleistocene assemblage at McKittrick may have existed at approximately the same time or a little later.



Fig. 3. Number of individuals in each species of bird represented by five or more individuals at Carpinteria.

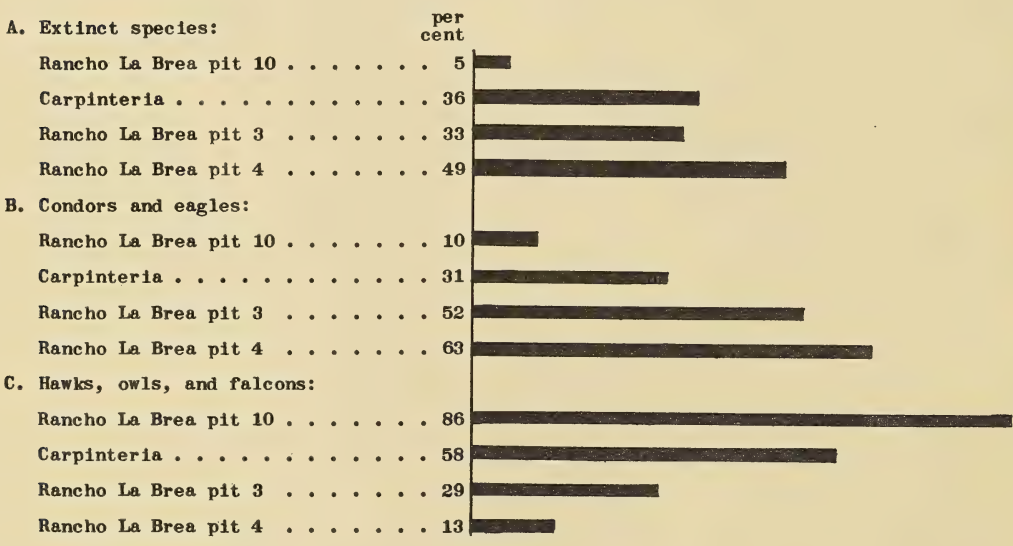


Fig. 4. Comparison of the avifaunas of Carpinteria and Rancho La Brea. Graphic representation of the percentage of (A) individuals of extinct species relative to the total avifauna, (B) condors and eagles, and (C) hawks, owls, and falcons relative to the total rap-torial count. Figures for Rancho La Brea pits modified after Howard and Miller (1939).

SUMMARY

The entire Pleistocene avifauna of Carpinteria, as represented in the collections of the Santa Barbara Museum of Natural History, California Institute of Technology, and University of California at Los Angeles, is reviewed in

order to obtain the best possible basis for comparison with the assemblages from Rancho La Brea and McKittrick, California.

The present survey of the fossil avifauna substantiates the view that the Carpinteria asphalt traps were situated in a forested region like that now existing in the Monterey Peninsula, 200 miles farther north. Half of the species with known habitat preferences are those usually found in wooded areas, and more than a third have a preference for brushy regions. Of the six species represented by young birds as well as mature individuals, three are brush dwellers.

Comparison with the living avifauna of the Point Lobos Reserve, Monterey County, reveals some similarity between the environment of that area and the inferred environment at Carpinteria during the Pleistocene, but with the woodland or forest influence greater and the shore-line influence distinctly less at the latter locality.

Comparison of the Carpinteria assemblage with the Pleistocene avifaunas of Rancho La Brea and McKittrick suggests that both McKittrick and Carpinteria are slightly younger than Rancho La Brea. Differences in environment in the immediate vicinity of the asphalt deposits, however, apparently affect the composition of the faunas to such an extent that this factor must be taken into consideration when the three faunas are compared.

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CONTRIBUTIONS TO PALEONTOLOGY

V

A TERTIARY MAMMALIAN FAUNA FROM THE SAN ANTONIO
MOUNTAINS NEAR TONOPAH, NEVADA

PAUL C. HENSHAW

With eleven plates and seven text figures

[Issued January 15, 1942]

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A TERTIARY MAMMALIAN FAUNA FROM THE SAN ANTONIO MOUNTAINS
NEAR TONOPAH, NEVADA

INTRODUCTION

Discovery of fossil mammals near Tonopah, Nevada, affords opportunity not only to date significant geologic events in the west central part of the state, but also to describe the plains life of the region during Upper Miocene time. The fauna contains nineteen species, six of which are known from no other locality. Close association of the mammalian assemblage with remains of diatoms, mollusks, and fishes in the stratigraphic record establishes a definite correlation in time between these groups. The value of the discovery as a record of Upper Miocene life is greatly enhanced by the simultaneous occurrence in a limited area of these two entirely different and complementary facies of contemporary faunas, representing arid plains and inland lake. This association furnishes interesting and detailed information as to the paleogeography of the region. Abundance of individual mammals from a quarry of narrow horizontal and vertical limitations provides a large unmixed fauna on which to base paleoecological studies.

The fossil mammal occurrence in the San Antonio Mountains was discovered in 1922 by H. G. Ferguson, of the U. S. Geological Survey. A letter from Mr. Ferguson under date of March 9, 1940 gives the following interesting statement concerning the discovery and development of this fossil site:

I found the locality in the summer of 1922 during the course of reconnaissance mapping of the Tonopah Quadrangle. The discovery was purely accidental, and not the result of any systematic search. The fossils were abundantly exposed at the surface in a bed of greenish marl about two feet thick and traceable along the strike for something over 100 feet. Someone, probably a prospector, had been there before me, as there was a shallow hole cut with a pick. Evidently he was not interested. I made a small collection, chiefly of teeth, and these were later identified by Dr. Gidley. Later in the season another collection was made. . . . I later gave Dr. Stock a note as to the locality and still later showed the place to Mr. H. C. Clinton, a mineral collector at Manhattan, Nevada. Mr. Clinton collected at the site before Dr. Stock's party, and I believe exchanged fossils for minerals with different museums and universities. When I revisited the site in 1937 with Professor Muller of Stanford, I was astonished at the large-scale mining done by the California Tech. party.

In 1931 and 1932 field parties of the California Institute of Technology carried on quarrying operations in the most productive parts of the fossil-bearing horizon. In 1939, in the course of a brief geological reconnaissance of the area, A. B. Drescher relocated an invertebrate horizon near by which had been described by Spurr. In addition, Drescher discovered the fossil remains of fish at approximately the same horizon.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the advice and counsel of Dr. Chester Stock, whose indispensable aid and critical reading of the manuscript have been a constant source of encouragement and inspiration. I am indebted to E. L. Furlong, who prepared much of the material and furnished many valuable suggestions. R. W. Wilson kindly contributed a statement regarding the fossil rodents and lagomorphs in the collection. For their courtesy, cooperation, and helpful suggestions I am obligated to the staff of the Museum of Paleontology, University of California. The illustrations were prepared by David P. Willoughby.

LOCATION OF FOSSIL MATERIAL

The fossil material in the Tonopah collection was found at the California Institute of Technology Vertebrate Paleontology locality 172 (plate 1). The locality lies on the western flank of the San Antonio Mountains, approximately 9 miles north of Tonopah, Nevada. The area where the fossiliferous strata are exposed is located at a point 3.67 miles N. 39° W. of Mineral Monument No. 206, U.S.G.S. topographic map of the Tonopah Quadrangle, Nevada, edition of 1908, reprinted 1922 (see fig. 1).

HISTORICAL REVIEW

In 1866 William P. Blake read before the California Academy of Sciences a short notice pointing out that "fossilized fish are found in a light colored clay shale in the mountains a few miles north of Silver Peak." He displayed a few of the specimens, but did not venture to identify them.

The first published notice of extensive fresh-water deposits in the Silver Peak region appears to be that of M. A. Knapp, a mining engineer. Knapp (1897) described particularly the coal deposits occurring in beds at the north end of the Silver Peak Range. Molluscan remains collected by Knapp near the coal beds were examined by J. C. Merriam, of the University of California, who identified *Campeoloma* sp., *Unio* sp., *Planorbis* like *spectabilis* Meek, and *Ancylus* like *undulatus* Meek. He suggested that the shells were early Miocene or late Eocene in age.

H. W. Turner (1900a) named and briefly described the Esmeralda formation. In his more complete report published later in the year, Turner (1900b) described the stratigraphy and structure of the Esmeralda formation in detail. He estimated the total thickness of the beds at 14,800 feet.

F. H. Knowlton (1900) examined a florule collected by Turner at two localities in the Esmeralda formation. These fossil plants embraced fourteen forms, all but one regarded as new. Most of the new forms were found referable to well known living genera. Knowlton assigned no geological age to the florule.

F. A. Lucas (1900a, 1900b) described as a new species, *Leuciscus turneri*, a small fish obtained by Turner in the Esmeralda deposits of the Silver Peak

Quadrangle. In the title of one of the published notices (1900a), Lucas suggested that the species was Miocene in age.

J. E. Spurr (1905, pp. 51-55), in the study of the Tonopah mining district, defined the Siebert tuff (lake beds) as consisting of white stratified tuffs, beautifully and uniformly bedded, and composed of well sorted material. He

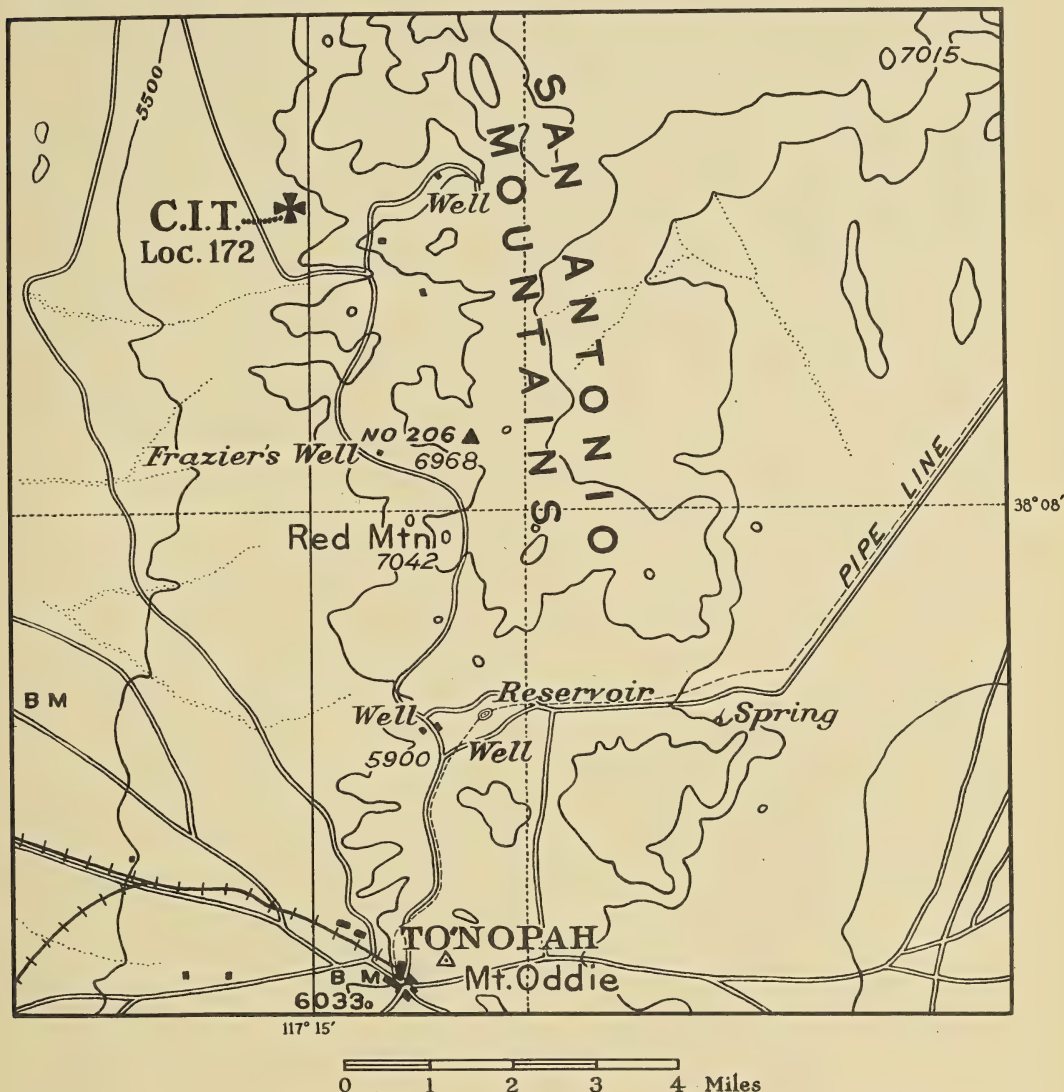


Fig. 1. Part of the southeastern quarter of the Tonopah Quadrangle, Nevada, showing location of Upper Miocene vertebrate fossil quarries (Calif. Inst. Tech. Vert. Pale. Loc. 172) in the San Antonio Mountains. Contour interval, 500 feet.

noted that where beds of conglomerate occur the pebbles are perfectly rounded. The principal deposits include several hundred feet of lake beds of consistent fine-grained character containing fresh-water infusoria. Sandy and cross-bedded sediments were considered to represent shore and delta facies. Spurr concluded that the lake must have been of considerable size from the fact that over 600 feet of lake beds are exposed on Siebert Mountain, with neither top nor bottom

present. He hypothesized that the lake basin originated from a crustal depression that followed volcanic activity and was perhaps coupled with a climatic change to increased rainfall. The sedimentary materials were derived mostly from glassy dacites and rhyolites. Limited deposits of volcanic ash and small lava flows indicate that mild vulcanism continued during deposition of the lake beds. Upper beds of river gravels, some of which contain petrified wood, indicate uplift and renewed erosion of the highlands and mark the conclusion of lacustrine deposition.

From some of the tuffs Spurr collected infusoria which were identified by R. M. Bagg, Jr., as *Galltonella granulata* Bailey, *Galltonella varians* Agardh, and *Coscinodiscus radiatus* Ehrenberg.

In the same publication, Spurr (1905, pp. 66-67) mentions a locality 8 miles north of Tonopah and 1 mile west of the little mining camp of Ray where there occurs a series of folded gravels, tuffs, lavas, and some white, thin limestones carrying numerous Eocene fossils. W. H. Dall noted that the fossils are like those from the Wasatch or Bear River Laramie Eocene of White and Meek. They are: *Vivipara* near *V. couesi*, *Planorbis utahensis* Meek, *Ancylus?* sp., and *Corbicula?* cf. *Sphaerium idahoense* Meek. Of *Corbicula* Dall remarked that "the specimens are merely internal casts, but if they are really *Corbicula* they may prove to be *C. occidentalis* Meek. Their condition is too imperfect to be certain even of the genus, but the form closely approaches that of the figures of *S. idahoense*." Spurr states further: "These [beds] overlie the Paleozoic limestones near Ray. Similar beds were noted at several places between Ray and Sodaville." He intimated that they are probably continuous with a part of the Tertiary deposits of the Silver Peak and Monte Cristo mountains.

Following Spurr's intensive study of the Tonopah region, S. H. Ball (1907), F. L. Ransome (1907, 1909), and later Adolph Knopf (1921) applied the term Siebert formation to a series of volcanics and lake beds in widely scattered localities throughout west central Nevada and eastern California. H. G. Ferguson (1924) has pointed out that all these authors failed to restrict the name Siebert formation to Spurr's definition. All of them extended the formation to include equivalents of Spurr's underlying Fraction breccia. Ferguson suggested that the Esmeralda formation of Turner is the approximate equivalent of the Fraction breccia and Siebert tuff combined.

Harold Hannibal (1912) summarized the Recent and Tertiary fresh-water Mollusca of the California province. He included a number of species recorded from the Truckee Lake beds, Nevada. For the new species which he described as *Viviparus turneri*, Hannibal cited several localities in the vicinity of Silver Peak.

Junius Henderson (1935, p. 225), in reviewing the fossil nonmarine Mollusca of North America, points out with regard to Hannibal's contribution of 1912 that "his synonymies and classification in this paper are notably erroneous." Henderson deleted all species of indefinite locality from Hannibal's list of forms

from the Truckee beds and combined the remainder with the molluscan fauna reported by Turner from the type Esmeralda. Following is his list of Mollusca (Henderson, 1935, p. 46): from the Esmeralda beds, Silver Peak region, Nevada, *Unio* sp., *Sphaerium catherinae* Hannibal, *Planorbis cordillerana* (Hannibal), *Lanx* like *undulatus* (Meek), *Viviparus turneri* Hannibal; from the Truckee beds, Hawthorne, Nevada, *Pisidium?* *meeki* Hannibal.

J. P. Buwalda (1914) described the Esmeralda formation in considerable detail as it occurs in Stewart and Ione valleys in the vicinity of Cedar Mountain, Nevada. He discussed the distribution, lithology, thickness, stratigraphic relations, and structure of the formation. Mammalian fossil material collected from the Esmeralda by Buwalda and Baker was studied by J. C. Merriam. The fossil mammalian remains, according to Buwalda (1914), "are most abundant in sandstones and in ashy deposits; a portion of a single connected skeleton was found in limestone. A few specimens were found in beds of coarse angular terrestrial material." The age of the fauna was determined as approximately Upper Miocene. Buwalda identified four species of fresh-water mollusks in the collections from the Esmeralda beds in Ione and Stewart valleys: *Heliosoma cordillerana* Hannibal, *Viviparus turneri* Hannibal, *Melania* near *sculptilis* Meek, *Corneocyclas meeki* Hannibal. Buwalda traced the beds in Ione Valley by continuous outcrops to the type Esmeralda locality, and found the first two of the molluscan species named above occurring in abundance in the type section.

Merriam (1916a) reported on the fauna of the Cedar Mountain region collected by Buwalda and Baker. The literature on the region was reviewed. Merriam drew largely on the published observations of Buwalda's geological reconnaissance for his information on the Cedar Mountain beds and the relation of the fauna to its environment. Mention was made of two fishes examined by J. O. Snyder, a salmonlike form and a cyprinoid; a testudinate, possibly *Clemmys*; and three ducks identified by L. H. Miller as *Nettion carolinense* (Gmelin), *Marila collaris* (Donovan), and *Querquedula cyanoptera* (Vieillot)?. In his discussion of the faunal relationships, Merriam noted that the mammals included elements of both primitive and advanced types, and suggested that more than one fauna might be represented. He compared the stage of the fauna to that of the Barstow and Santa Fe.

In 1924 S. H. Cathcart assembled a small collection of fossil plants from the Esmeralda. The fossils were taken from a coal prospect 4 miles southeast of Morgan Ranch and 15 miles west of Hawthorne, Mineral County, Nevada. E. W. Berry (1927) combined his findings with those of Knowlton and presented a revised floral list of the Esmeralda formation. Berry considered that the known "flora does not furnish conclusive evidence regarding the regional environment." He compared the Esmeralda flora with that of Florissant, Mascall, Latah, and Payette, and concluded that the Esmeralda is "not older than Middle Miocene and is almost certainly Upper Miocene."

Axelrod (1940) on the basis of recent collections of later Tertiary floras in the Great Basin province pointed out that the Esmeralda flora as described

by Knowlton is distinct from the Coal Valley flora reported by Berry. Axelrod revised and added to the Esmeralda flora. He demonstrated that the assemblage shows a close relation to the flora now living in southern Arizona and in the middle Kern River Canyon area. He ascribed a Lower Pliocene age to the Esmeralda flora and suggested that the Coal Valley flora is Uppermost Miocene.

Further collecting in the Cedar Mountain area and discovery of fossiliferous strata in Fish Lake Valley renewed interest in the faunas of the Esmeralda beds. Reports on various finds followed in quick succession (Matthew, 1929; Burt, 1929; Hall, 1929; Stirton, 1929; Hall, 1930b, 1930c). Stirton (1932) summarized the results of a study of the new material in conjunction with a re-study of the earlier University of California collections. He found that at no single locality does a mixed fauna occur. A lens of brown sandstone containing fossils of the older *Merychippus* fauna occurs at a locality distinct from those characterized by the younger *Plihippus-Hipparton* fauna. Stirton noted that the fossils of the older fauna give evidence of having been reworked. The older Cedar Mountain fauna was designated Middle Miocene in age. The Fish Lake Valley fauna was considered Lower Pliocene and equivalent to the Upper Snake Creek of Nebraska. A comparison of the Fish Lake Valley and late Cedar Mountain faunas indicates that these assemblages are of the same age or closely related.

In subsequent publications Stirton (1933, 1936; Teilhard and Stirton, 1934) used the old name Esmeralda to designate the Lower Pliocene mammalian remains from the Fish Lake Valley and Cedar Mountain areas. Stewart Spring was suggested as a name for the Middle Miocene fauna obtained at U.C. locality 2027 (Teilhard and Stirton, 1934, p. 285) in the Cedar Mountain area. At the same time, Stirton stated definitely that "*Merychippus* teeth clearly indicate that the Stewart Spring fauna is, approximately, equivalent to the Virgin Valley and not as advanced as the Santa Fe."

California Institute of Technology locality 172, which was discovered by Ferguson, has yielded an abundant fauna. Furlong (1934) briefly commented on the locality and described two new species of *Merycodus* in the fauna.

Bode (1934, pp. 56, 59) compared the crown heights of upper and lower merychippine cheek teeth obtained in faunas from the Mascall, *Merychippus* zone at Coalinga, Barstow, and Tonopah.

In a paper read before the Paleontological Society, Pacific Coast Branch, Stock (1934) described the skull and dentition of *Pseudaelurus intrepidus* from Tonopah. Stock (1935, p. 1067, fig. 2c) compared the lower deciduous molars of *Merychippus calamarius* (C.I.T. no. 1827) from Tonopah with those in a section of jaw of *Plihippus tehonensis* taken from a well core in the Chanac formation, California.

In the present study a description is given of the remaining species in the fauna as represented by the collections of the California Institute of Technology. An attempt is also made to demonstrate the relations of the fauna to other Tertiary mammalian assemblages of western North America.

GEOLOGIC OCCURRENCE AND NOMENCLATURE OF FOSSIL BEDS

The deposits containing the mammalian fauna are those which Spurr visited and described (1905, pp. 66-67), 8 miles north of Tonopah (fig. 1) and 1 mile west of the mining camp of Ray (see above). Though Spurr did not find the vertebrate fossils, he collected shells from near-by Tertiary limestones.

Stratigraphy

Approximately 1 mile east of C.I.T. Vertebrate Paleontology locality 172 the Tertiary lake beds are found in fault contact with Paleozoic limestones. At several localities in the cores of anticlinal folds in the immediate vicinity of the mammalian fossil deposit, the beds can be seen to overlies pre-Esmeralda lavas.

The section at locality 172 was estimated from near-by exposures to be approximately 40 feet thick.

Thickness
(feet)

2-3	Dendritic calcareous tufa
4-5	Gray-green silts, gravelly sandstone, occasional chert. Extremely abundant mammalian remains
25	Gray tuffaceous sediments
5 (est.)	Conglomerate with pebbles of green and red volcanic rocks in green matrix
Base	Unknown

The locality where Spurr collected fossil invertebrates is situated approximately $\frac{3}{4}$ mile due east of C.I.T. locality 172. The section containing the invertebrates is somewhat thicker.

Thickness
(feet)

1	Dendritic tufa tubes and pipes
30	Punky gray shale
20	Alternating thin layers of light gray tuffaceous sandstone, light gray punky shale, white coquina, fine angular gravel, light-colored calcareous sandstone. Very great abundance of invertebrate fossils
30 (est.)	White to gray soft shale
Base	Unknown

A third roughly measured section is located on the south side of the first important wash to the south of C.I.T. locality 172. It lies slightly more than $\frac{1}{2}$ mile south of C.I.T. locality 172, and approximately $\frac{3}{4}$ mile southwest of Spurr's invertebrate locality. The section here is even thicker than at the latter.

Thickness
(feet)

4-6	Dendritic tufa domes and pipes
35	Light gray, poorly bedded shales
0.75	Resistant gray sandy tuff
15	Light gray shale
1	Dense, resistant, gray-white, tuffaceous shale. <i>Marker bed</i>
85	White, thin-bedded to laminated, diatom-bearing shale
Base	Andesitic volcanics cut by breccia dikes

At about $\frac{1}{4}$ mile northeast of the locality where the third section was measured, the basal shales show a gray-buff facies not so thinly bedded as the laminated shales of the measured section. Thirty feet below the resistant 1-foot *marker bed* these gray-buff shales contain abundant fish remains along with some fossil plant material.

At still another locality situated almost equidistant from the localities of the three measured sections, fish remains similar to those mentioned above occur intimately associated with invertebrates of the types which are found at Spurr's locality.

In the vicinity of all the fossil-bearing localities, the weather-resistant dendritic tufa beds form the highest remaining horizon. To the west of C.I.T. locality 172 lies a considerable thickness of gently tilted buff sandstones which are thought to be younger than the thin fossiliferous series.

Structure

California Institute of Technology locality 172 lies near the north side of a basin, slightly over a mile wide and about 3 miles long, which reaches into the west flank of the San Antonio Mountains. Esmeralda sediments underlie most of the area within the basin. A few scattered outcrops of pre-Esmeralda lavas are exposed in the main wash where down-cutting and lateral planation have stripped away the overlying lake beds. The eastern end of the basin is bounded by a fault contact with the Paleozoic rocks. To the north of the basin the Esmeralda sediments are overlain with angular unconformity by Pliocene (?) andesite. On the south the narrow basin is bounded by rhyolite which Ferguson regards as post-Esmeralda Upper Miocene in age.

The fossil-bearing strata have been folded along east-west axes into two synclines and an anticline. The steepest dips are less than 25° . All the flexures plunge gently eastward toward the main front of the San Antonio Mountains.

Several minor transverse faults striking west of north have locally displaced the folded strata. A longitudinal fault along which the south side has moved east a few hundred feet lies almost on the axial plane of the anticline. This minor faulting probably occurred at the time of the folding of the sediments.

Molluscan and Piscine Faunas

In addition to the mammalian remains, the fossils obtained from the Tertiary lake beds north of Tonopah comprise a considerable number of molds and casts of four species of fresh-water mollusks. The anterior part of one fossil fish and an abundance of fish bones and scales were also found.

The Mollusca have been tentatively identified. They represent the same four species which Spurr collected and Dall identified. Revised list: *Pisidium?* *meeki* Hannibal; *Planorbis* cf. *cordillerana* (Hannibal), small, diameter 16 mm.;

Lanx cf. *undulatus* (Meek), large, length 20 mm.; and *Viviparus turneri* Hannibal. All these species are apparently lacustrine in habitat (Hannibal, 1912).

These Mollusca are closely allied to, although not identical with, species in the molluscan fauna described by Buwalda (1914) from the Esmeralda of Ione and Stewart valleys. *Planorbis* cf. *cordillerana* differs from *Planorbis cordillerana* in its smaller size and more deeply umbilicate shell. There is a similar close relationship yet lack of identity between this San Antonio Mountain fauna and the molluscan fauna of the type Esmeralda which was examined by Merriam (Turner, 1900b, pp. 203-204).

A single fossil fish in the collection has been referred to *Leuciscus turneri* Lucas. Absence of the caudal and anal fins, and the poor preservation of the remaining skeletal parts, render impossible any detailed comparison with the type of the species from near Silver Peak.

On the basis of an extensive geological reconnaissance of the area, H. G. Ferguson (written communication) includes all these deposits in the Esmeralda formation. Ferguson remarks that "the beds have the same position relative to older and younger formations as in Turner's type locality, though, of course, there is not continuous outcrop between the two areas." The similarity of the molluscan and piscine fauna of the San Antonio Mountain Esmeralda beds to the corresponding assemblage of the type Esmeralda adds support to the correlation made by Ferguson.

OCCURRENCE AND PRESERVATION OF FOSSIL MATERIAL

Local Correlation

The mammalian fossil material was recovered from stratified beds of gray-green silt and sandy silt in which occur lenses of gravelly sandstone and occasional beds of chert. Although the fossil mammal horizon is limited in vertical extent to less than 10 feet, fossil float was found continuously along the weathered outcrop for more than $\frac{1}{2}$ mile to the southwest and south of the producing quarries. This strict stratigraphic limitation of the fossil-bearing horizon proclaims the purity of the mammalian fauna. The invertebrates and fishes are likewise strictly limited as to stratigraphic horizon. The invertebrate-bearing marls and light gray shales total not more than 20 feet in thickness. All the fossiliferous localities, both vertebrate and invertebrate, occur stratigraphically beneath the dendritic tufa layer, and presumably lie not far above the local base of the Esmeralda sediments. It is believed that the faunas of all these San Antonio Mountain localities are essentially contemporaneous.

Lacustrine Facies

The large extent of the sedimentary deposits and the thickness of the diatom-bearing beds indicate the existence of a lake of considerable size in Upper Miocene time. The light-colored shales and marls of the fish and invertebrate

localities must have been deposited out in the lake far enough from shore to escape admixture with coarser stream-borne sediments. Sporadic volcanic activity showered the lake and surrounding country with fine gray ash, much of which was incorporated in the offshore sediments of the lake. The marl, diatomite, and tufa of the lacustral beds were deposited by organic and chemical action.

Salinity of the Miocene Lake

The layer of dendritic tufa noted at the top of each measured section appears to be identical in character with similar deposits of Lake Lahontan, described in detail by Russell (1885). Tufa tubes, pipes, and hollow domes are extremely common in the horizon. For similar structures in Mono Lake and the Lahontan basin, Russell suggested two possible modes of origin: "First, by the direct precipitation of calcareous tufa about nuclei. Second, from the precipitation of the same material from springs rising in lakes that are highly charged with mineral matter in solution." From the presence of abundant normally developed molluscan shells embedded in the dendritic tufa, Russell concluded that the waters of Lake Lahontan were not strongly alkaline or saline when that deposit was laid down. By analogy, the Upper Miocene Esmeralda lake may have been somewhat saline but not greatly so when the dendritic tufa was formed.

The presence of the fresh-water mollusks and fish indicates that at least occasionally the waters were not too saline for animal life to exist. Under the heading "Syntonia" Hannibal (1912, pp. 114-116) discusses the effect of various salines on molluscan life. He notes that whereas magnesium compounds produce remarkable physiological effects and act as poisons, even high concentrations of sodium, potassium, and calcium salts have little effect. Hence, waters saline enough to form precipitates (e.g. dendritic tufa and chert) may still support normal or almost normal molluscan faunas.

Though *Leuciscus* is predominantly a fresh-water fish in both Europe and North America, many members of the genus are found in the brackish waters of the Baltic Sea and in bays of the eastern and western shores of the Atlantic. Accordingly, it is assumed that although *Leuciscus turneri* may be primarily a fresh-water type, this fish could persist for a time at least under conditions of increasing salinity.

Delta Facies

The gray-green silts, sands, gravels, and occasional cherts enclosing the mammalian fossils are indicative of a near-shore deposit, perhaps deltaic in character. The occasional layers of chert interbedded with the silts may provide significant evidence as to the nature of the environment at the time of deposition. According to Twenhofel (1939), the normal environment for chert

interbedded with clastic sediments, particularly clays and silts, is an area where fresh silica-bearing waters mingle with saline water. Ideal conditions for such a deposit would be found adjacent to an entrance of a stream into a saline lake.

Preservation of the Fossils

All the fossil material from C.I.T. locality 172 is highly silicified. Most of the unweathered specimens are tinted with the distinctive green color of the surrounding sedimentary formation.

A few of the teeth in the collection are definitely rounded as though they had been rolled and abraded either by stream transportation or by wave action near a lake shore. Most of the fossil material, however, shows no post-mortem wear whatsoever. In many cases, delicate tooth structures have been preserved with great fidelity.

The fossil material consists almost entirely of dentitions and limb bones. Out of a collection representing more than 225 individuals, only a single cat skull and a few antelope frontlets were preserved well enough to merit description. Equally noteworthy is the almost complete absence of vertebrae and ribs.

During the course of excavation at C.I.T. locality 172 two maps of the major quarry site were made on a scale of 1 inch to 1 foot. All fossil finds within the first 6 feet below the surface were plotted on one map, and finds from 6 to 10 feet below the surface were recorded on the second. These maps form an important record of the fossil occurrence. The productive part of the quarry covered an area of approximately 40 feet on the strike of the beds and 50 feet down the dip. Over 80 per cent of the fossils were derived from the upper horizon of the quarry, a 3-foot zone extending from 3 to 6 feet below the surface of the ground. The maps give no indication of any special orientation of the fossil bones, nor is there any suggestion of channels determining the localization of bones within the quarry. It must be remembered, however, that the entire quarry may represent a channel of concentration 40 feet wide in the half-mile outcrop of sparsely fossiliferous to barren beds.

The quarry maps do reveal the relatively high degree of association of the fossil bones. Dentitions and limb bones of the same individual were not found in association except in a few doubtful cases. Associations of maxillae and rami and of various bones of the same limb, however, are frequent. Invariably the lateral metapodials of the feet of horses are intimately associated with the medial metapodial. Furthermore, the metapodials are often closely associated with carpals and tarsals and occasionally with parts of the upper limb bones. The dentitions, though still associated, are more widely scattered. For example, the left maxilla and dentition of a rhinoceros was separated by a distance of 2 feet from the left ramus and dentition, and a tooth from the right ramus of the same individual was found 8 feet away in the same horizon.

Association and distribution of the kind noted appears to indicate that the osseous material arrived at the locality still held together by ligaments. Furthermore, burial must have been relatively rapid to prevent any wide scattering of the osseous material.

FAUNAL CENSUS AND ENVIRONMENT

Of the 225 individuals in all stages of growth represented in the collections of the California Institute of Technology, 195 are herbivores. Except for 1 insectivore and a number of uncouneted rodents and lagomorphs, the remainder of the fauna consists of carnivores. Less than 20 of the individuals are young animals.

CENSUS OF TONOPAH MAMMALIAN FAUNA

Genus	No. individuals
Metechinus	1
Tomarctus	9
Leptocyon	6
Aelurodon	4
Amphicyon?	2
Brachypsalis	3
Pseudaelurus	5
Hypohippus	12
Merychippus	110
Aphelops?	3
Alticamelus?	8
Merycodus	62

(Rodentia and Lagomorpha not included)

This distribution of genera approaches the normal conditions which might be expected in a plains habitat. In contrast, attention may be directed to the faunas of Rancho La Brea (Stock, 1929) and McKittrick (Schultz, 1938), where an unnatural preponderance of carnivores occurs. The tar pools of Rancho La Brea most certainly functioned as baited traps for unwary carnivores. Though the McKittrick assemblage approaches more normal ecological conditions, the concentration of carnivores is still extremely high; hence, McKittrick likewise must have acted to some extent as a carnivore trap. The Tonopah fauna comes closer to furnishing a normal cross section of mammalian life as it existed at the stage when the deposits were laid down. The balance appears still to remain in favor of the predators, however, for there are 11 individuals in the fauna representing *Aelurodon*, *Amphicyon*, and *Pseudaelurus*.

In the attempt to reach an estimate of the number of herbivores which ought to be present in the assemblage on the basis of the carnivore population, certain assumptions are perhaps permissible. For example, at least one major kill had to be made each day to satisfy the hunger of the predatory group. We may assume also that the horses and antelopes, which

furnished most of the food, produced offspring but once a year. On this basis, a normal population for a given moment in time must contain more than 365 herbivores for every 11 large carnivores. Yet in the Tonopah fauna we find a ratio of only 195 to 11. It may be concluded, therefore, that in the collections from Tonopah the carnivore-herbivore ratio is still abnormally high. Probably the smallest representation occurs in the antelope family. This ordinarily prolific group is represented by only 60-odd individuals.

The abundance of grazing horses (*Merychippus*) and antelopes, coupled with the occurrence of camels and long-limbed rhinoceroses, indicates without question that the environment was one of grassy, perhaps shrub-covered plains. It has often been suggested that *Hypohippus* was a browser, not a grazer. The relative number of individuals of this genus is small. Perhaps the hypohippines foraged in stream bottoms or along the edges of the lake, where doubtless there flourished shrubs and trees to their liking.

CONDITIONS OF ACCUMULATION AND BURIAL

Summarizing the conclusions drawn from the geological and faunal evidence, we find that the fossils occur in delta deposits along the shores of a large saline lake. The mammals probably died near their burial place. The bones were quickly covered, before they could be scattered far. The species represented in the fauna are predominantly of a plains-dwelling type.

A saline lake and a plains fauna suggest aridity of climate. In an arid region, the occurrence of occasional droughts is extremely probable. During a severe drought the larger mammals are forced to congregate about the more permanent water holes. In this instance the lake, and perhaps the lower reaches of a stream entering the lake, furnished the last available sources of water in the district. Perhaps famine coupled with the depredations of the carnivores decimated the assembled multitude. With the coming of rain, stream-borne silts and sands buried the carcasses before the bones became widely scattered.

COMPOSITION AND STAGE OF EVOLUTION OF FAUNA

Representatives of the family Erinaceidae are rare in the later Tertiary record of western North America. Only two species have been described thus far, *Metechinus nevadensis* and *Meterix latidens* from the Fish Lake Valley Lower Pliocene of California. *Metechinus fergusoni* differs from all other erinaceids (Leche, 1902) except *M. nevadensis* in the extreme reduction of its tooth row. It parallels *M. nevadensis* in many details of the dentition and tooth structure. On the basis of the less complete reduction of the upper premolars in *M. fergusoni*, the latter is regarded as slightly more primitive than *M. nevadensis* from Fish Lake Valley.

In his introductory statement concerning the Tonopah Rodentia and Lagomorpha, Wilson states that this part of the fauna is late Miocene or early

Pliocene in age. The content and relationships of the faunule, namely, "*Mylagaulus*" sp., cf. *Eutamias ateles* Hall, cf. *Peromyscus longidens* Hall or possibly n. sp., and *Hypolaemus* sp., suggest that it is most closely related to the Barstow.

Tomarctus paulus from Tonopah differs from Matthew's *T. confertus*, and from material referred to that species by Matthew, in slightly larger size and in the more slender proportions of the teeth. It is doubtful whether C.I.T. no. 1229 is closely related to the Lower Snake Creek type. Even if close relation between the two species were established, it would still be difficult to determine the relative stage of advancement of each form.

Tomarctus? kelloggi of the Tonopah fauna agrees closely with the type specimen from Virgin Valley. The only possibility of determining the phylogenetic position of this species rests on the questionable assumption that the second lower molars U.C. no. 10651 and U.C. no. 12542, of the Virgin Valley and Thousand Creek mammal beds respectively, are correctly referred to *T. kelloggi*. Without the accompanying lower carnassials it is impossible to demonstrate that these teeth are "relatively large" and "extraordinarily developed." If Merriam was correct in referring both these teeth to *T. kelloggi*, the following argument may have a little weight. M_2 , C.I.T. no. 789, is slightly smaller over all and is slightly more constricted between trigonid and heel than is U.C. no. 10651 from Virgin Valley. M_2 from Thousand Creek, U.C. no. 12542, referred by Merriam to *T. near kelloggi*, shows even more constriction and is still smaller. If this crown constriction and diminution in size of M_2 mark an evolutionary trend, the Tonopah form lies between *T. kelloggi* of Virgin Valley and *T. near kelloggi* of Thousand Creek.

Tomarctus brevirostris, represented in the Tonopah collection by a canine and a single lower carnassial tooth, conforms almost exactly to Pawnee Creek and Lower Snake Creek material which has been referred to Cope's species.

Leptocyon vafer shows no specific difference from Leidy's type, and agrees perfectly with Matthew's description of the Lower Snake Creek form. The Tonopah material is smaller than the referred specimen from Ricardo, which differs further in having an entoconid in M_1 .

Evidence discussed in detail below indicates that the varietal form *Aelurodon wheelerianus asthenostylus* differs markedly from typical Aelurodons of the Ricardo, Esmeralda, and Barstow faunas. The Tonopah variety appears to approximate an undescribed *Aelurodon* from Barstow, and to be closely allied to Cope's relatively primitive type *A. wheelerianus* from Santa Fe. *Aelurodon wheelerianus asthenostylus* is differentiated by extreme weakness of the parastyle on P^4 .

The *Amphicyon?* metapodials are comparable with some undescribed material in the Pawnee Creek collection of the University of California. Since canid metapodials change relatively slowly in character, it is doubtful whether further light could be shed on the position of the Tonopah *Amphicyon?* even if similar material were present in other faunas.

Brachypsalis pachycephalus of the Tonopah represents an evolutionary stage close to that of *B. modicus* of Lower Snake Creek, and appears to be cospecific with Cope's type from the Loup Fork Upper Miocene. An undescribed specimen from the Barstow collection of the University of California (U.C. no. 35447) closely resembles C.I.T. no. 1231.

Pseudaelurus intrepidus is very closely allied to Leidy's type from Niobrara River. Referred specimens from Lower Snake Creek are similar. The Barstow material differs in being more massive. A lower jaw from the Avawatz Mountains is definitely more advanced.

Hypohippus near *affinis* may be slightly more primitive than referred material from the Burge of Gordon Creek, Nebraska, and more advanced than referred material in the University of California Niobrara River collection.

The relationships of *Merychippus calamartus* are discussed at length below. The form has close affinities with the same species from Barstow, but seems a little more advanced in its greater crown height and more complex enamel pattern. On the basis of its highly complex enamel pattern, the Santa Fe type may be more advanced in turn than the Tonopah form.

Aphelops? cristatus, n. sp., is apparently definitely more advanced than the Pawnee Creek *A. megalodus*, and considerably more primitive than *A. mutilus* from the Coffee Ranch and Higgins Quarry A.

The peculiar *Alticamelus? stocki*, n. sp., presents a difficult problem in phylogenetic position. It may correspond roughly in evolutionary stage to *A. leptocolon* in the Lower Snake Creek and the Pawnee Creek faunas.

The relationships of the unusual and primitive merycodonts, *Merycodus loxocerus* and *Merycodus hookwayi*, are likewise difficult to demonstrate. These species have no counterparts in either the Barstow or the Ricardo fauna. In fact, no similar forms have been reported from any part of the North American Tertiary. Since they are both characterized by primitive dentitions coupled with a previously unrecorded type of horn core, it appears that these forms represent an aberrant development from a primitive type which persisted locally.

RELATIONSHIPS OF FAUNA

Great Basin

The wealth of material in the Tonopah collection renders feasible detailed comparisons with other well represented faunas of southeastern California and western Nevada (fig. 2).

The Tonopah rodent and lagomorph faunule is close to the Barstow. *Tomarctus brevirostris* may be near the Barstow *T.* near *temerarius*. At least one of the Barstow Aelurodons resembles closely the Tonopah *A. wheelerianus asthenostylus*. *Pseudaelurus* sp. of the Barstow differs somewhat in its more massive jaw from the Tonopah form. An undescribed *Brachypsalis* from Barstow has close affinities with the slightly smaller Tonopah specimen. *Hypohippus* near *affinis* occurs

in the Barstow fauna, but the fragmentary nature of the material precludes any conclusive determination of relationship. The most advanced merychippines of the Barstow are certainly very close to *Merychippus calamarius*

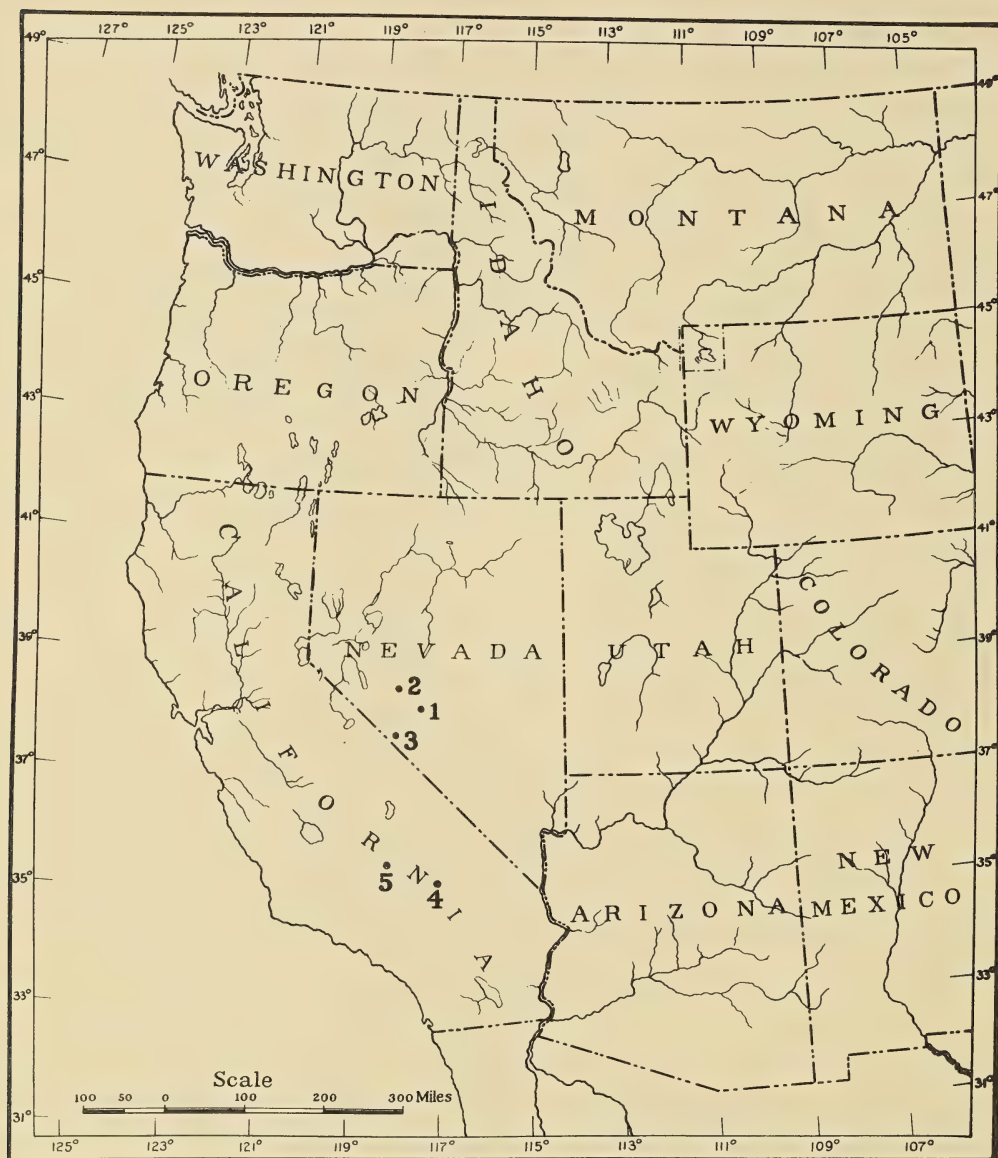


Fig. 2. Location of Upper Miocene and Lower Pliocene vertebrate fossil localities in the southern Great Basin province. 1, Tonopah; 2, Cedar Mountain; 3, Fish Lake Valley; 4, Barstow; 5, Ricardo.

from Tonopah. *Alticamelus alexandrae* seems more advanced than the primitive-appearing *A.?* *stocki* of Tonopah. The Tonopah merycodonts are likewise relatively primitive, more so perhaps than any of the Barstow forms except *Ramoceros* (*Merriamoceros*) *coronatus*.

In summary, the only demonstrable difference which may be indicative of the relative geologic ages of the Tonopah and Barstow faunas appears in the Equidae. *Merychippus calamarius* constitutes one of the most advanced merychippine forms to be recorded from the North American Tertiary, but the advance of this form beyond the stage represented by the Barstow species is very slight. It is interesting to note that an undescribed series of merychippine upper cheek teeth found in one of the uppermost horizons of the Barstow by Clair Steggall, of the University of California at Los Angeles, is as advanced as *M. calamarius* in crown height, although it lies in the *M. intermontanus* line.

Detailed comparison demonstrates clearly that the Fish Lake Valley fauna (Esmeralda of Stirton, 1932) represents a stage of evolution more advanced than that of the Tonopah. Interest centers in the occurrence of an insectivore in the Tonopah fauna, because this type appears to be closely related to *Metechinus nevadensis*. *Metechinus fergusonii* shows considerably less reduction of the premolar teeth and consequently seems definitely more primitive than *M. nevadensis*. The rodent and lagomorph faunule of Tonopah appears to be slightly more primitive than the Fish Lake Valley assemblage. *Aelurodon haydeni* from Fish Lake Valley shows larger size and perhaps more progressive characters than the Tonopah *Aelurodon*. *Hypohippus* near *affinis* shows characters in which it is assuredly more primitive than, if not directly ancestral to, *H.* near *nevadensis* of Fish Lake Valley. *Neohipparion* cf. *occidentale* and *Pliohippus* cf. *leidyani* of Fish Lake Valley are much more advanced than *Merychippus calamarius* from Tonopah. The primitive camel and merycodonts of the Tonopah fauna show no close affinities with the fragmentary Fish Lake Valley material.

Without exception, the members of the Ricardo mammalian assemblage clearly display an advance in evolutionary stage over comparable species from Tonopah. *Canis? vafer* of the Ricardo is larger than the Tonopah species. The Ricardo *Aelurodon*s typically bulk much larger than *A. wheelerianus asthenostylus*. One undescribed Ricardo *Aelurodon*, slightly larger than the Tonopah species, is unfortunately too fragmentary to permit a close comparison. The relatively large lower jaw of *Aphelops* sp. (Stock and Furlong, 1926) from the Ricardo represents a form probably more advanced than the Tonopah species. The Ricardo Equidae include several species of *Hipparion* and *Pliohippus* and typify a stage of evolution considerably later than that of *Merychippus calamarius* from Tonopah. Fragmentary camelid material from Ricardo affords no satisfactory comparison with *Alticamelus? stocki*. *Merycodus (Paracosoryx) furlongi* is much more advanced in its dentition than either of the Tonopah species.

Tomarctus? kellooggi from Tonopah may be roughly equivalent to *T.* near *kellooggi* from Stewart Spring (Stirton, 1932; Teilhard and Stirton, 1934, p. 285). The Stewart Spring Equidae, however, consist of *Hypohippus* near *osborni* and *Merychippus isonesus*, and are much more primitive than *H.* near *affinis* and *M. calamarius* respectively from Tonopah.

Pacific Coast

No known forms in the Mint Canyon fauna (Maxson, 1930; Stirton, 1933) are at all comparable with the Tonopah species. The Nevadan fauna is considered definitely younger than the Tick Canyon (Jahns, 1939), and it appears to be older than the Hipparion zone of the Upper Mint Canyon. Further finds in the Mint Canyon series may reveal a faunal zone comparable with that occurring near Tonopah.

The Quatal Canyon fauna (Gazin, 1930; VanderHoof, 1939) offers no comparable species.

The Chanac fauna (Merriam, 1915, 1916b; Stock, 1935) has been divided on the basis of its Equidae into an upper and lower part (Stirton, 1939a, p. 135). The Lower Tejon Hills (Drescher, 1941), characterized by *Nannippus tehonensis* and *Pliohippus tehonensis*, seems definitely more advanced than the Tonopah.

The Lower Pliocene fauna of the San Francisco Bay region (Merriam, 1913a, 1917; Stirton, 1935, 1939b) corresponds closely to that of the Tejon Hills and accordingly is definitely younger than the assemblage from Nevada.

Great Plains

In the absence of any revision of the Santa Fe fauna it is impossible to make a satisfactory comparison at this time. Frick (1933) states that the Santa Fe beds, as determined by mammalian fossils, range in age from Middle Miocene to Pleistocene. *Aelurodon wheelerianus asthenostylus* is smaller than and not identical with the type *A. wheelerianus* of Santa Fe. *Aphelops meridianus* from New Mexico seems more primitive than the Tonopah *A. ? cristatus*. The Tonopah *Merychippus calamarius* appears almost identical with Cope's type from the Santa Fe. Out of the abundance of merycodont types reported by Frick from the Santa Fe, none belong to the subgenus *Merycodus* (*Paracosoryx*) into which both of the Tonopah species seem to fall. Future exploration in the valley of the Rio Grande will doubtless reveal a series of distinct faunas, some of which may well be contemporary with the Tonopah.

On the basis of the distinctly more primitive forms *Aphelops ceratorhinus* and *Merycodus agilis*, the Madison Valley fauna of Montana (Douglass, 1900) is regarded as pre-Tonopah in age.

Specimens from the Niobrara River, namely *Hypohippus* cf. *osborni*, *Merychippus republicanus*, *M. insignis*, and *M. perditus*, in the collections of the University of California are all more primitive than *H. near affinis* and *M. calamarius* from Tonopah.

The Burge fauna (McGrew, 1938) in the collections of the University of California includes *Hypohippus affinis*, *Neohipparion coloradense*, *Nannippus* cf. *retrusus*, and *Pliohippus* cf. *supremus*, and typifies an evolutionary stage more advanced than that of the Tonopah. Both the Niobrara River and the Burge faunas included members of the genus *Metechinus*. If future exploration yields more

diagnostic material representing the latter genus, it will be of some significance to determine in detail the relation of the Great Plains species to the Tonopah and the Fish Lake Valley material.

The relations between the Tonopah fauna and other Tertiary mammalian assemblages known from North America are shown in the accompanying chart.

RELATION OF THE TONOPAH FAUNA TO MIOCENE-PLIOCENE VERTEBRATE
HORIZONS OF WESTERN NORTH AMERICA

Age	Nevada	California	New Mexico	Montana	Nebraska
Lower Pliocene		Ricardo			
	Esmeralda				Burge
Upper Miocene	Tonopah	Barstow	Santa Fe		
				Madison Valley	Niobrara River
	Stewart Springs				

For lists of the Tonopah and Barstow faunas see the following page.

Faunal Lists

TONOPAH FAUNA

Metechinus fergusoni, n. sp.

"*Mylagaulus*" sp.

Cf. *Eutamias ateles* Hall

Cf. *Peromyscus longidens* Hall or
possibly n. sp.

Hypolagus sp.

Tomarctus paulus, n. sp.

Tomarctus? *kelloggi* (Merriam)

Tomarctus brevirostris Cope

Leptocyon vafer (Leidy)

Aelurodon wheelerianus asthenostylus, n. var.

Amphicyon? sp.

Brachypsalis pachycephalus Cope

Pseudaelurus intrepidus Leidy

Hypohippus near *affinis* (Leidy)

Merychippus calamarius (Cope)

Aphelops? *cristalatus*, n. sp.

Alticamelus? *stocki*, n. sp.

Merycodus loxocerus Furlong

Merycodus hookwayi Furlong

BARSTOW FAUNA

Insectivora

Limnoecus tricuspis Stirton

Rodentia

Eutamias ateles Hall

Perognathoides cf. *tertius* Hall

Perognathoides sp.

Heteromyid gen. and sp.

Peromyscus longidens Hall

Peromyscus sp.

Peromyscus sp.

Lagomorpha

Hypolagus cf. *vetus* L. Kellogg

Hypolagus sp.

Carnivora

Tomarctus near *temerarius* (Leidy)

Canid (*Canis?*) sp. small

Aelurodon near *wheelerianus* Cope

Aelurodon, *Dinocyon*, or *Amphicyon* sp.

Brachypsalis sp.

Machaerodont sp. a

Machaerodont sp. b

Machaerodont sp. c

Felid? indet.

Pseudaelurus sp.

Proboscidea

Tetrabelodon? sp.

Perissodactyla

Hypohippus near *affinis* (Leidy)

Parahippus? *mourningi* Merriam

Merychippus *intermontanus* Merriam

Merychippus calamarius stylodontus Merriam

Merychippus sumani Merriam

Protohippus? or *Pliohippus?* sp.

*Artiodactyla**Tayassuidae*

Prosthennops? sp.

Merycoidodontidae

Merycochoerus buwaldi Merriam

Camelidae

Procamelus sp. a

Procamelus sp. b

Pliauchenia sp.

Alticamelus alexandrae Davidson

Cervidae

Dromomeryx or *Cervus?* sp.

Antilocapridae

Ramoceros (*Paramoceros*) *brevicornis* Frick

Ramoceros (*Merriamoceros*) *coronatus* (Merriam)

Merycodus (*Paracosoryx*) *alticornis* (Frick)

Meryceros *joraki* Frick

SYSTEMATIC DESCRIPTION

ERINACEIDAE

Part of a shattered left maxillary with the anterior part of the zygomatic arch, and most of a left ramus of the same individual, comprise the insectivore material from Tonopah. The teeth which are present include C and P⁴ and P₄-M₂. All these teeth are excellently preserved. The teeth show resemblance to those of a hedgehog and more particularly to those of the genus *Metechinus* from the Fish Lake Valley beds. On the basis of apparent differences in tooth structure, the material is described as belonging to a new species. It gives me great pleasure to name this species for Henry G. Ferguson, of the U. S. Geological Survey.

Metechinus fergusoni, n. sp.

(Plate 2, figures 1-2b)

Type specimen. A part of the left maxillary, C.I.T. no. 2817 (pl. 2, figs. 1, 1a, 1b), and a part of the left ramus bearing most of the tooth row, C.I.T. no. 2817 (pl. 2, figs. 2, 2a, 2b). The maxillary shows part of the alveoli for two incisors, C, the roots of P³?, P⁴, part of the alveolus of M¹, and the anterior part of the zygomatic arch. The lower jaw shows three anterior alveoli, one of which is partially closed, P₄, M₁, M₂, and part of the lower posterior portion of the ramus.

Specific characters. Small size. Upper canine with two distinct roots. P³ present, not caducous. P⁴ with very high, large metacone blade. P₄ well developed, with two distinct roots and slightly complex crown. M₁ with very long trigonid.

Skull. The infraorbital foramen lies just anterior to P⁴. The anterior part of the zygomatic arch arises from the maxillary at a point external to the anterior root of M¹.

Mandible. The lower border of the mandible is almost flat beneath P₄-M₂, curving gently upward anteriorly and posteriorly. The part of the ramus posterior to M₂ is long, whereas that in front of this tooth is considerably shortened. The major part of the ascending ramus is missing; the ridge at the lower anterior edge of the part which is present makes a sharp anterior boundary for the masseteric fossa. The inferior boundary of this fossa is very weak. A large mental foramen lies below P₄. The mandibular foramen lies in the almost smooth internal surface of the ramus. Depth of mandible below M₁, 2.8 mm.; width of mandible below M₁, 1.7 mm.

Upper dentition. A sharp-cusped tooth with small anterior basal cusp and strong basal heel cusp is tentatively regarded as a canine. Low cingula border the base of the tooth near these cusps. The tooth has two distinct roots.

P³ is represented by two roots set diagonally in the jaw. The antero-external root is larger than the posterointernal.

In P^4 the long metacone blade is almost as high as the backward-sloping sharp-pointed paracone, and is approximately equal to it in total bulk. The metacone blade is strongly developed and extends posteroexternally. Two inner cusps, of equal height, arise from a common internal platform and are further connected by a low internal cingulum. The posterior border of the cingulum curves well back, giving a large areal extent to the posterior part of the internal platform.

Two upper incisors appear to be represented by the internal borders of their alveoli. Of M^1 only the alveolus of the anteroexternal root is present. Since M_2 is present in the mandible, a second molar must have been present in the upper series, although no trace of it is preserved.

Lower dentition. P_4 , supported by two separate roots, is set obliquely in the jaw. The principal cusp is moderately high and suggests that in its unworn state the tip was divided into two very small cuspules, the posterior one located slightly external to the anterior one. The cingulum, rising high and strong on the anterior and posterior borders of the crown, forms almost an anterior basal cusp and a cusp on the heel.

M_1 has a long trigonid and is relatively very large. The long, slender paraconid blade is curved gently inward, and is more anteroposterior than transverse in position. The protoconid is strong, high, and separated from the almost equally large metaconid by a very shallow valley. The low-set heel is basined and bears a hypoconid and entoconid of equal size. A moderately strong cingulum extends along the external side of the tooth from the anterior part of the protoconid to the middle of the base of the hypoconid.

M_2 is much smaller than M_1 and bears a short paraconid with anteroposterior shear. The protoconid and metaconid cusps are of equal size. The small heel is narrower than the trigonid. The hypoconid equals the entoconid in size. A low cingulum lies along the external side of the tooth and extends from the anterior end of the tooth to the middle of the base of the hypoconid.

Of the three anterior alveoli, the very large, oval, almost horizontal one is considered to be for I_2 ; the small, partially closed one contained a caducous I_3 ; and the large, round one immediately anterior to P_4 held the lower canine. These assumptions are open to question, but they are in accord with such information as is available on loss of teeth in the family Erinaceidae (Leche, 1902). M_3 is absent.

Comparative measurements (in millimeters) of dentition of Metechinus fergusoni

Upper dentition:	C.I.T. no. 2817	U.C. no. 29600
C, anteroposterior diameter	1.2	...
C, transverse diameter	0.7	...
P^4 , anteroposterior diameter	3.2	4.5
P^4 , transverse diameter	2.3	4.2

Comparative measurements - Continued

Lower dentition:	C.I.T. no. 2817	U.C. no. 29600
Length of series P_4-M_2	6.2	10.1*
P_4 , anteroposterior diameter	1.4	1.5
P_4 , transverse diameter	1.1	...
M_1 , anteroposterior diameter	3.0	5.3
M_1 , transverse diameter	1.7	2.7
M_2 , anteroposterior diameter	1.9	3.6
M_2 , transverse diameter	1.2	2.2
M_2 , width of heel	0.9	1.9

*Composite.

Relationships. The position of *Metechinus fergusoni* from Tonopah is definitely within the family Erinaceidae. Detailed comparison with the modern *Erinaceus europaeus europaeus* from Germany and *Neotetracus sinensis* from Ho-mu-shu Pass, China, reveals many striking similarities and a few important differences in dentition.

Meterix latidens Hall (1929) from Fish Lake Valley bulks larger and has a much more nearly complete dental battery. It also differs in having two mental foramina and a strong ridge on the posterointernal face of the ramus.

Metechinus nevadensis Matthew (1929) from Fish Lake Valley shows a close similarity to the Tonopah form. The two species agree in the reduction of the premolars and the posterior molars, and in the corresponding enlargement and specialization of M_1 . The dental formulas are probably identical. That in specimen C.I.T. no. 2817 may be recorded as follows:

$$\frac{? \ 2 \ . \ 1 \ . \ 2 \ . \ ?}{2 \ . \ 1 \ . \ 1 \ . \ 2}$$

In both species M_2 is much smaller than M_1 , and M_3 is absent. All these points of agreement are in characters designated by Matthew as of generic rank. The forms differ in two generic characters given by Matthew: (1) P^3 of *M. nevadensis* is caducous, whereas it is less reduced in C.I.T. no. 2817; (2) P_4 of *M. nevadensis* is small and simple; in the Tonopah erinaceid it is larger and more complex.

Some of the minor differences between C.I.T. no. 2817 and *M. nevadensis* are as follows: In the Tonopah species the upper canine is less reduced and more complex in pattern; P_4 is relatively longer and narrower and has a relatively higher and larger metacone blade; and P_4 is much less reduced and slightly more complex. Except for the slightly longer paraconid blade and the external cingulum in M_1 from Tonopah, the two molars of both species are in close agreement. The most obvious difference between the two forms is that in size, C.I.T. no. 2817 being only about 60 per cent as large as *M. nevadensis*.

Perhaps none of these differences can be considered of generic rank. All but two of them lie in the same direction, that is, increase in total size accompanied by reduction of anterior premolars and posterior molars, perhaps indicative of an evolutionary trend from the Tonopah species to *Metechinus*

nevadensis. The two features in *M. fergusoni* which seem relatively more advanced than in *M. nevadensis* are really one and the same: the relatively greater anteroposterior length of P^4 and of M_1 in C.I.T. no. 2817.

Though the Tonopah form may later be given generic distinction, temporarily at least it is referred to Matthew's genus *Metechinus*.

RODENTIA AND LAGOMORPHA

By Robert W. Wilson

This small and fragmentary collection includes three rodents and a lagomorph. In age, the Tonopah assemblage is closest perhaps to the Barstow fauna, but identification of the several types is tentative. A late Miocene or early Pliocene age is suggested rather strongly by the collection. A provisional list of forms is as follows: "*Mylagaulus*" sp.; cf. *Eutamias ateles* Hall; cf. *Peromyscus longidens* Hall, or possibly n. sp.; *Hypolagus* sp.

"*Mylagaulus*" sp.

A mylagaulid is represented by a palate with P^4 , M^2-M^3 of both sides, and several isolated cheek teeth. Until a thorough revision of the mylagaulids is undertaken, a more specific determination is hardly possible.

Cf. *Eutamias ateles* Hall

The presence of a small sciurid is recorded by several isolated cheek teeth, an incisor fragment, and two pieces of ramus each with a single cheek tooth. The Tonopah species apparently is closer to *Eutamias ateles* of the Barstow than to any other form, although it is not certain that the two are cospecific. Chipmunks are rare as fossils, and the present occurrence apparently is only the second record of these squirrels in the North American Tertiary. Perhaps it is open to question whether either of these forms can be referred to the living genus.

Cf. *Peromyscus longidens* Hall, or possibly n. sp.

A cricetid type, close to the Barstow *Peromyscus longidens*, but possibly representing a new species, is known by the following: skull fragment with incisor and M^1-M^3 , maxillary fragment with M^1-M^2 , two isolated molars, and several bits of rami with not more than a single cheek tooth in each.

Hypolagus sp.

A partial skull with dentition, a cheek-tooth series comprising right P^2-M^1 , a left ramus with P_3-M_3 , and various individual teeth are to be assigned to the very common later Tertiary leporid *Hypolagus*. In size,

the material indicates a species smaller than *H. vetus*, and more nearly agreeing with *H. limnetus* from the Hagerman and *H. cf. vetus* from the Fish Lake Valley beds. The Tonopah species probably represents an undescribed if not hitherto unknown form. In several characters of the dentition, such as relatively simple enamel folding of the upper cheek teeth, it apparently is somewhat more primitive than Middle Pliocene and later leporids. The species is no more primitive, however, than its stratigraphic position would suggest.

CANIDAE

Fossil remains of the Canidae in the Tonopah collection represent a surprisingly large variety of forms. The well preserved, almost complete dentition of a young adult described as the species *Tomarctus paulus* is the best specimen in the collection. Part of a lower jaw and a few lower teeth are referred to the species *Tomarctus? kelloggi*. *Tomarctus brevirostris* and *Leptocyon vafer* are represented by more or less fragmentary material. Two jaws, part of a palate, and a few separate teeth are designated as a new variety, *Aelurodon wheelerianus asthenostylus*. An interesting pair of large canid metacarpals and a phalanx are referred to *Amphicyon*. If properly assigned to this genus, they furnish the first real clue to the foot structure of that type.

Tomarctus paulus, n. sp.

(Plate 2, figures 3-4a)

Type specimen. A palate with well preserved, complete dentition; a complete lower jaw of the same individual with all teeth except I_1 , C.I.T. no. 1229 (pl. 2, figs. 3, 4, 4a).

Referred material. A few separate upper teeth and a number of partial rami complete the collection. No skeletal parts have been referred to this species. A minimum population count based on rami totals five individuals.

Specific characters. Size of *Tomarctus confertus* (Matthew). P^4 elongate with protocone set very far forward. Upper molars very wide transversely. Lower dentition differs from *T. confertus* type in narrower premolars with only moderately high cusps. M_1 short, not compressed. M_2 moderately long and narrow.

Skull. All that can be determined from the poorly preserved skull material is that the posterior part of the palate was relatively wide as compared with that of *Canis latrans* (47 mm. least over-all diameter across the palate immediately posterior to P^4). The infraorbital foramen lies over the anterior end of P^4 .

Mandible. The mandible is fairly well preserved except for the anterior part of the symphysis, the tip of the coronoid process of the right ramus, and the ascending left ramus. The ramus is slender, but not so slender as that of

a fox or coyote. The anterior mental foramen lies below P_1 ; the posterior below the middle of P_3 . In C.I.T. no. 1229, the length from condyle to alveolus for I_1 is approx. 90 mm.; minimum over-all diameter from lower border of ramus to tip of coronoid process, approx. 35 mm. The depth of the ramus below M_1 in this specimen is 14.7 mm., the width 7.3 mm.; in C.I.T. no. 1232 the corresponding measurements are 17.3 and 8.5 mm. Although the mandible of no. 1232 is of an older individual and is much more massive than that of no. 1229, the dentition is of the same size.

Upper dentition. The incisors are small. All these teeth, even I^3 , characteristically bear accessory tubercles on either side of the principal cusp, and a cingulum behind. The canine is short and slightly stouter than that of *C. latrans*.

All the premolars have a slight backward cant to the principal cusp. The single-rooted P^1 has a small posterior accessory cusp but no anterior one. P^2 and P^3 are both double-rooted and have small heel cusps as well as posterior accessory cusps. P^3 bears a definite anterior accessory cusp on the internal side, but P^2 has no such cusp.

The carnassial is long, but relatively not so narrow as in *C. latrans*. A small parastyle lies on the anterior border. The strong protocone is sharply set off from the rest of the tooth and stands well forward of the anteroexternal border.

M^1 and M^2 are very similar to these teeth in *Canis*, with the exception that their heels are slightly larger.

Lower dentition. The small incisors resemble those of *Canis* in every way. The canine is proportionally shorter and stouter.

Single-rooted P_1 has a simple conical cusp. P_2 , P_3 , and P_4 are all double-rooted. Each bears a posterior accessory cusp and a heel cusp; P_4 has a slight suggestion of an anterior accessory cusp.

M_1 is doglike in almost every respect. The tooth is less elongate than in *Canis*, and the metaconid is proportionally slightly larger. M_2 is proportionally larger than in *Canis*. It bears the distinguishing paraconid, and its entoconid is well developed. M_3 bears an anterior paraconid crest, well marked protoconid and metaconid cusps, and a posterior hypoconid-entoconid crest. The roots of the tooth have coalesced to form a single root which is extremely elongate anteroposteriorly.

Measurements (in millimeters) of dentition of Tomarctus paulus, C.I.T. no. 1229

Upper dentition:

Length of series I^1 - M^2	60a
Length of series P^1 - M^2	45.5
C, anteroposterior diameter	6.4
C, transverse diameter	3.9
P^1 , anteroposterior diameter	3.6
P^1 , transverse diameter	2.2
P^2 , anteroposterior diameter	6.0
P^2 , transverse diameter	3.2

a, approximate.

Measurements - Continued

Upper dentition - continued:

P ³ , anteroposterior diameter	7.5
P ³ , transverse diameter	3.5
P ⁴ , anteroposterior diameter on external side . . .	13.0
P ⁴ , anteroposterior diameter on internal side . . .	14.9
P ⁴ , transverse diameter	6.5
M ¹ , anteroposterior diameter	9.8
M ¹ , transverse diameter	13.2
M ² , anteroposterior diameter	6.0
M ² , transverse diameter	9.6

Lower dentition:

Length of series I ₁ -M ₃	65a
Length of series P ₁ -M ₃	51a
C, anteroposterior diameter	4.1
C, transverse diameter	4.1
P ₁ , anteroposterior diameter	2.9
P ₁ , transverse diameter	2.0
P ₂ , anteroposterior diameter	5.4
P ₂ , transverse diameter	3.0
P ₃ , anteroposterior diameter	6.5
P ₃ , transverse diameter	3.5
P ₄ , anteroposterior diameter	7.7
P ₄ , transverse diameter	4.0
M ₁ , anteroposterior diameter	15.0
M ₁ , transverse diameter	6.0
M ₂ , anteroposterior diameter	7.6
M ₂ , transverse diameter	5.0
M ₃ , anteroposterior diameter	4.0
M ₃ , transverse diameter	3.0

a, approximate.

Relationships. Comparisons show that a close relation exists between *Tomarctus paulus* and *T. confertus* (Matthew, 1918, pp. 188-189, fig. 1) from the Snake Creek *Merychippus paniensis* zone. *Tomarctus confertus* has a slightly shorter tooth row and smaller teeth; its premolars are slightly shorter and wider, and M₁ is much more compressed. On the other hand, M₂ is slightly larger than the comparable tooth in C.I.T. no. 1229. In a skull referred to *T. confertus* by W. D. Matthew (1924, pp. 96-97) the upper dentition is slightly smaller than in C.I.T. no. 1229; P⁴ is less elongate and the protocone does not stand so far forward. The upper molars of A.M.N.H. no. 18253, although of approximately the same anteroposterior diameter, are much shorter transversely than in C.I.T. no. 1229.

If the specimen shown in Leidy's figure (1869, pl. 1, fig. 12) were taken as the type of *T. temerarius* as Matthew suggests (1924, p. 98), then all material which corresponds to the large upper jaw fragment described but unfigured by Leidy would be excluded from the species. On the basis of page priority, however, it is deemed advisable to consider the larger unfigured upper jaw material as the type of Leidy's species *T. temerarius*. Hence, the relatively large jaw from Barstow referred by Merriam (1919) to *T. near temerarius* does not resemble the type and is certainly not conspecific with *Tomarctus paulus*.

On the other hand, C.I.T. no. 1229 agrees very closely in size and cusp

arrangement with Leidy's figure of M_1 . Furthermore, the depth of ramus below M_1 of Leidy's figure falls between the values recorded for *T. paulus*.

All other material referred to *Tomarctus* represents species of much larger size.

Tomarctus? kelloggi (Merriam)

(Plate 3, figures 1-2a)

A partial ramus bearing P_1 - M_1 , C.I.T. no. 1235 (pl. 3, figs. 1, 1a), a ramal fragment with M_1 and M_2 , C.I.T. no. 789 (pl. 3, figs. 2, 2a), and separate M_1 and M_2 differ in several important respects from other canids of this group. At least three individuals are represented by this material.

Mandible. The ramus, deep beneath P_1 , becomes still deeper below M_2 . To some extent this depth is attributable to the advanced age of the individual. In spite of its depth, the mandible does not attain very great thickness. The symphyseal region appears to have been relatively small. The masseteric fossa does not reach as far forward as M_2 . In C.I.T. no. 1230, the depth of the mandible below P_3 is 22.0 mm.; depth of mandible below M_2 , 26.0 mm.; thickness of mandible below M_2 , 9.2 mm.

Lower dentition. The lower teeth are well spaced and uncrowded. The moderate-sized premolars have suffered little reduction. M_1 appears relatively short, and M_2 inordinately long.

P_1 , single-rooted and peglike, is nevertheless rather large. P_2 , P_3 , and P_4 are all two-rooted and progressively increase in size. P_2 is simple. P_3 bears a small heel cusp. P_4 has a small posterior accessory cusp as well as a strong heel cusp.

M_1 in C.I.T. no. 1235 is much worn on its external side by a crushing and grinding action without much shear. A referred unworn specimen, C.I.T. no. 789, is of almost identical size. It bears a short, blunt paraconid, a blunt, heavy protoconid, and a relatively very large rounded metaconid high up on the protoconid cusp and closely appressed to it. On the heel the large entoconid, which closely resembles the hypoconid in size, occupies a more elevated position than the latter. A small tubercle lies between the base of the protoconid and the hypoconid. The external base of the heel is expanded, making the heel the widest part of the tooth.

The extremely large second lower molar is 80 per cent as long as M_1 , but appears to be characteristically canid. A protoconid of moderate size, a paraconid almost as strong as the protoconid, and a very large and elevated metaconid constitute the trigonid. The long, basined heel bears the hypoconid and entoconid cusps, both well developed. A small tubercle lies in the valley between the protoconid and the hypoconid. The cingulum is developed into a prominent ridge on the anteroexternal side of the trigonid. Between trigonid and heel, the external wall is strongly indented and the internal wall is slightly indented, giving the tooth a pronounced "waist." The enamel of the posterior face of the tooth is abraded slightly owing to contact with a third molar.

Comparative measurements (in millimeters) of dentition of *Tomarctus? kelloggi*

	C.I.T. no. 1235	C.I.T. no. 789	U.C. no. 11562 Virgin Valley
Length of series P ₁ -M ₁	45.6
P ₁ , anteroposterior diameter	3.9
P ₁ , transverse diameter	2.5
P ₂ , anteroposterior diameter	6.5	6.0
P ₂ , transverse diameter	3.4
P ₃ , anteroposterior diameter	7.3	6.7
P ₃ , transverse diameter	3.6
P ₄ , anteroposterior diameter	8.4	8.4
P ₄ , transverse diameter	4.7
M ₁ , anteroposterior diameter	13.5	13.0	15.0
M ₁ , transverse diameter	6.9	6.6	7.0
M ₂ , anteroposterior diameter	10.5	10.5
M ₂ , transverse diameter	5.9	6.7

Relationships. The completely canid appearance of the lower dentition, combined with the presence of a well developed paraconid in M₂, corresponds to the characteristic features of the genus *Tomarctus*. The most striking peculiarities are the depth of the ramus, the simplicity of the premolars, the anteroposterior shortness of M₁, and the relatively great length of M₂.

Although *Tomarctus temerarius* and *T. paulus* approach C.I.T. no. 1235 in size, they differ strikingly in the proportions of M₁ and M₂. In fact, all but one of the species assigned to the genus *Tomarctus* have a large to very large lower carnassial and a small to very small M₂. The one species *T. ? kelloggi* (Merriam, 1911b) differs from all others in having an M₂ "relatively large and extraordinarily developed." Merriam's species from Virgin Valley agrees closely with the Tonopah material. The jaw is "relatively heavy in the posterior half." The jaw of C.I.T. no. 1235 is still heavier, but it has been mentioned already that the extreme depth of jaw (for a canid) of no. 1235 may be partly explained by the age of the individual. The premolars are slightly larger and more massive in C.I.T. no. 1235. M₁ and M₂ of C.I.T. nos. 1235 and 789 agree in almost every detail with the type of the species. The paraconid of M₁ is not quite so long as in U.C. no. 11562.

The posterior part of a lower carnassial, U.C. no. 19767, from Stewart Spring (Merriam, 1916a) is probably conspecific with the Tonopah material although slightly smaller.

Any comparison with referred M₂'s U.C. no. 10561 from Virgin Valley and U.C. no. 12542 from Thousand Creek (Merriam, 1911b) would have limited value in view of the fact that such reference is far from indisputable.

On the basis of the extremely long and slender M₂, and the low-crowned M₁ with pairs of subequal cusps, the species *T. ? kelloggi* may be regarded as generically distinct from *Tomarctus*. Additional material, especially of the maxillary dentition, will undoubtedly throw further light on this question.

Tomarctus brevirostris Cope

(Plate 3, figures 3-4a)

A much worn M₁, C.I.T. no. 774 (pl. 3, figs. 4, 4a), is like a coyote molar in size and resembles the comparable tooth in *Tomarctus brevirostris*.

The tooth is moderately large and differs from those of other members of the genus in its exceptionally long heel. Tooth wear has undoubtedly accentuated the heel length.

A long, slender upper canine tooth, C.I.T. no. 2853 (pl. 3, fig. 3), has also been referred to this species.

Measurements (in millimeters) of dentition of Tomarctus brevirostris

C.I.T. no. 2853

C, upper, anteroposterior diameter	5
C, upper, transverse diameter	2.5
C, upper, distance from tip of crown to end of root	3.8

No. 774

M ₁ , anteroposterior diameter	19.5
M ₁ , transverse diameter	7.6
M ₁ , anteroposterior diameter of heel	6.8

Relationships. *Tomarctus rurestris* (Condon) is distinctly larger than this form from Tonopah. *Tomarctus kelloggi* is much smaller. *Tomarctus temerarius* has a considerably smaller M₁ with a shorter heel. Of the canids described from the Great Plains region, *Tomarctus brevirostris* Cope (1873; Matthew, 1924, pp. 88-96, figs. 11-16) is nearest to the specimen from Tonopah. In size, proportions, metaconid development, and heel length, a specimen from Barstow (U.C. no. 19402) shows very close resemblance. The Barstow specimen was referred by Merriam (1919, pp. 462-464) to *T. near temerarius*. Matthew remarks that the type upper jaw of *T. temerarius* belongs to an animal only slightly smaller than the small variant *T. brevirostris*. The M₁ C.I.T. no. 774, which is a little larger than U.C. no. 19402 from Barstow, agrees almost exactly with M₁ of *T. brevirostris* from the Pawnee Creek and Lower Snake Creek.

Leptocyon vafer (Leidy)

(Plate 3, figures 6, 6a)

Both rami of a lower jaw, C.I.T. no. 780 (pl. 3, figs. 6, 6a), with some teeth missing combine to provide a series from C to M₂ complete except for P₄. Another lower jaw fragment, C.I.T. no. 2815, bears P₄-M₂. Additional lower jaw fragments, the posterior half of P₄, and a few milk teeth (poorly preserved C-Dm₄) make up the rest of the material representing this species. Five adults and one young individual are represented in the collection.

Mandible. The jaw is long, slender, shallow, and foxlike in appearance. The anterior mental foramen lies between P₁ and P₂, the posterior below P₃. Depth of mandible below middle of M₁, 10.5 mm.; thickness of mandible below middle of M₁, 5.2 mm.

Lower dentition. The long, slender canine is relatively larger than that in *Tomarctus paulus*. P₁ is single-rooted and simple-cusped. All the remaining premolars are double-rooted. P₂ has a simple cusp, P₃ a posterior accessory cusp, and P₄ a slight anterior basal cusp, a strong posterior accessory cusp, and a marked posterior basal cusp.

M₁ differs from this tooth in *T. paulus* in size and in presence of a low marginal entoconid crest rather than a strong entoconid cusp. This crest bears a very small entoconid. M₂ likewise differs strikingly from the corresponding tooth of *T. paulus*. It is characterized by an almost complete lack of paraconid and by a low entoconid crest bearing a minute entoconid. M₂ is followed by an alveolus for a single-rooted M₃.

Measurements (in millimeters) of dentition of Leptocyon vafer

	C.I.T. no. 780	C.I.T. no. 2815
Length of series C-M ₂	52.5
C, anteroposterior diameter	4.3
C, transverse diameter	3.0
P ₁ , anteroposterior diameter	2.2
P ₁ , transverse diameter	1.4
P ₂ , anteroposterior diameter	5.4
P ₂ , transverse diameter	1.8
P ₃ , anteroposterior diameter	6.6
P ₃ , transverse diameter	2.0
P ₄ , anteroposterior diameter	7.5
P ₄ , transverse diameter	3.0
M ₁ , anteroposterior diameter	10.5	10.8
M ₁ , transverse diameter	4.2	4.3
M ₂ , anteroposterior diameter	5.4	5.8
M ₂ , transverse diameter	3.5	3.4

Relationships. Although Leidy's type specimen *Leptocyon vafer* (1869, pl. 1, fig. 11) differs from the Tonopah form in having slightly larger proportions throughout, no apparent specific difference can be found to distinguish the two.

Leptocyon vafer from the Ricardo as described and figured by Merriam (1919, pp. 533-535, fig. 138a, b) is slightly larger and has an entoconid in M₁ which "is relatively small but prominent."

C.I.T. no. 780 is larger than Canid, indet., C.I.T. no. 2308, from the Avawatz Mountains (Henshaw, 1939, p. 17, pl. 2, figs. 2, 2a).

On the basis of the peculiar heel in M₁ of the Tonopah material, the author agrees with Matthew (1918, p. 190) that although the foxes parallel *L. vafer* in proportions of the jaw, they are "too closely related in dentition to *Canis* to be separately descended from *Leptocyon* instead of *Tephrocyon*" (*Tomarctus*), or from *Cynodesmus* (see McGrew, 1935, p. 310).

Aelurodon wheelerianus asthenostylus, n. var.

(Plate 4)

Type specimen. The posterior part of a palate with P⁴, M¹, and M², right and left, C.I.T. no. 781 (pl. 4, figs. 1, 1a); jaw of the same individual, C.I.T. no. 781 (pl. 4, figs. 2, 2a, 2b), lacking incisors, M₃, ascending rami, right P₁, and left M₁.

Referred material. A fragment of maxillary with M¹ and part of P⁴, C.I.T. no. 775; milk upper carnassial, C.I.T. no. 790; moderately complete

rami with dentition, C.I.T. no. 776; loose canines and premolars; a fragment of a radius and part of a calcaneum. At least two adults and one young individual are recorded.

Varietal character. Parastyle of P^4 very weak.

Mandible. The mandible is short, deep, and thick for a canid. Three mental foramina can be observed, the first a small one beneath I_3 , the second and largest beneath the anterior part of P_2 , and the third beneath the posterior part of P_3 . The deep masseteric fossa extends forward to a point below the posterior root of M_3 . Depth of mandible below middle of M_1 , 32.0 mm.; thickness of mandible below middle of M_1 , 12.9 mm.

Upper dentition. The upper carnassial tooth is relatively short and stout. It bears a parastyle in the form of a tiny tubercle which is not set off from the anterior part of the paracone. The strong protocone, located directly medial to the parastyle, does not project in front of the anteroexternal border of the tooth. A pronounced cingulum is present on the internal side of the heel.

M^1 is short anteroposteriorly and wide transversely. The heel is large, but there is no protoconule. The metaconule is relatively strong, being almost as well developed as the protocone. The hypocone crest is likewise well developed. A moderately strong cingulum traverses the anterior, external, and part of the posterior border of the tooth.

M^2 is relatively long anteroposteriorly and short transversely. All the cusps are small. In the heel only the protocone and hypocone are developed. A weak cingulum borders the anteroexternal part of the tooth.

A large, trenchant upper milk carnassial has the characteristic features of this tooth in canids. It bears only the faintest suggestion of a parastyle.

Lower dentition. The canine is short-crowned, stout, and heavy-rooted.

The lower premolar teeth are large and crowded. They tend to have a slight backward pitch. Individually these teeth show slight reduction in size, and are slightly compressed. P_1 in C.I.T. no. 781 is small and single-rooted. P_2 and P_3 are moderately large, double-rooted, and subequal in size. They are characterized by a large, conical main cusp and a small heel cusp, between which lies a distinct and moderately large posterior accessory cusp. There is a very small anterior accessory cusp on each tooth.

P_4 resembles P_2 and P_3 in form but is larger. The anterior end is toed in very slightly, giving the tooth an orientation not quite parallel to the jaw. The heel of the tooth differs from that of P_2 and P_3 in slightly greater transverse diameter.

M_1 , though massive, has no unusual features. M_2 has a small paraconid. M_3 is not preserved, but one ramus bears two small alveoli for its roots.

All teeth, both upper and lower, are moderately worn. There is little evidence of a shearing wear on the carnassials.

Comparative measurements (in millimeters) of dentition

	<i>A. wheelerianus</i> A.M.N.H. no. 8307*	C.I.T. no. 781	<i>A. saevus</i> A.M.N.H. no. 8305**
Upper dentition:			
P ⁴ , external anteroposterior diameter	23.2	21.2	23.8
P ⁴ , greatest transverse diameter	13a	12.6	12.5
M ¹ , external anteroposterior diameter	14.8	15.6	17.6
M ¹ , greatest transverse diameter	21.0	21.0	22.2
M ² , external anteroposterior diameter	7.4	8.1	6a
M ² , greatest transverse diameter	12.0	13.3	14.0
No. 790			
Dm ³ , anteroposterior diameter	16.8		
Dm ³ , greatest transverse diameter	9.0		
No. 781			
Lower dentition:			
Length of series C-M ₂96	100a	103
C, anteroposterior diameter at base of crown	12a	11.0	10.1
C, transverse diameter at base of crown	10a	8.8	8.5a
P ₁ , anteroposterior diameter	6.8	5.5	4.0
P ₁ , transverse diameter	4.6	3.9	3.3
P ₂ , anteroposterior diameter	10.8	9.2	9.1
P ₂ , transverse diameter	6.2	5.4	5.1
P ₃ , anteroposterior diameter	12.6	10.9	11.5
P ₃ , transverse diameter	7.4	6.5	6.5
P ₄ , anteroposterior diameter	16.4	14.2	16.1
P ₄ , transverse diameter	9.4	8.3	9.4
M ₁ , anteroposterior diameter	26.8	25.0	27.3
M ₁ , transverse diameter	12.4	10.2	11.5
M ₂ , anteroposterior diameter	11.0	11.8	12.8
M ₂ , transverse diameter	8.2	7.9	8.6

a, approximate.

*Matthew, 1904, figs. 3, 4.

**Cope and Matthew, 1915, pl. 118.

Relationships. *Aelurodon wheelerianus asthenostylus* of the Tonopah fauna falls apparently within the genus *Aelurodon* (see Matthew and Stirton, 1930, p. 182). Only in the fact that the parastyle in P⁴ is very weak does *A. w. asthenostylus* differ from the strong-styled type.

A very close relation appears to exist between *A. wheelerianus asthenostylus* and the type *A. wheelerianus* Cope from Santa Fe (Cope, 1877, pl. 69, type figs. 2, 2a, 2b; Cope and Matthew, 1915, pl. 119a; refiguration, Matthew, 1904, figs. 3, 4). In a recent publication VanderHoof and Gregory (1940) referred the latter specimen from the Great Plains to *A. taxoides*, pointing out that the material from New Mexico is too poorly preserved to define the species *A. wheelerianus*. No. 781 C.I.T. approximates the referred specimens very closely in size. *Aelurodon w. asthenostylus* has slightly reduced premolars and slightly enlarged molars. The anterior accessory cusps in the lower premolars are a little weaker in C.I.T. no. 781 than they are in the referred material A.M.N.H. no. 8307. P⁴ of the latter specimen bears a strong

parastyle, distinct from the anterior blade of the paracone. In *A. w. asthenostylus* the parastyle, no longer distinct, forms a weak anterior ridge on the paracone.

The ramus of the type *Aelurodon saevus* (Leidy, 1869, pl. 1, fig. 9; also Cope and Matthew, 1915, pls. 118-119; Matthew, 1904, figs. 3, 4) is longer and more slender, and its premolars are more widely spaced than in C.I.T. no. 781. The anterior mental foramen lies below the posterior root of P_2 in *A. saevus*. The latter species has been regarded by Matthew and Stirton (1930, p. 188) as a progressive derivative of *A. wheelerianus*. It shows in its dentition the same evolutionary trends as *A. w. asthenostylus*, carried out to a greater extent; it likewise ranks close to *A. w. asthenostylus* in size. The premolars of *A. saevus* are still more reduced; the molars are further enlarged. Anterior accessory cusps have disappeared completely; posterior accessory cusps are weaker. P^4 , however, does bear a parastyle. Thus *A. w. asthenostylus* with its weak parastyle seems to lie on a side branch near the primitive end of the direct line of evolution between *A. wheelerianus* and *A. saevus*.

Two rami from Barstow, U.C. nos. 19398 and 21231 (Merriam, 1919, p. 465, figs. 10, 11), have been referred to *Aelurodon* near *wheelerianus* Cope. Both are larger and more massive, but similar in proportions to *A. w. asthenostylus*. M_2 and M_3 of U.C. no. 19398 are proportionally very small; M_2 of U.C. no. 21231 is large. An undescribed *Aelurodon* from Barstow, U.C. no. 35295, is represented by a jaw which, although closely comparable with C.I.T. no. 781, is slightly smaller and more slender, with teeth slightly smaller, more trenchant, and not so closely spaced. This ramus bears only one mental foramen.

Aelurodon haydeni, U.C. no. 29638, from the Esmeralda of Fish Lake Valley, close to Leidy's type (1869, pl. 1, fig. 10), is more than one-third larger than *A. w. asthenostylus*.

Aelurodon aphobus Merriam (1919) is much larger than *A. w. asthenostylus*. A single undescribed lower jaw, U.C. no. 22472, from the Ricardo, though slightly larger, approximates C.I.T. no. 781 in size. The comparison can be carried no further, as the dentition of U.C. no. 22472 has not been preserved.

Amphicyon? sp.

(Text figure 3)

Metacarpals III and IV, C.I.T. no. 767 (fig. 3a), the distal end of another metapodial, C.I.T. no. 783, and a phalanx, C.I.T. no. 777 (fig. 3b), are characterized by very large size, massive appearance, and rugose surfaces. These foot elements are canid in appearance. Although the proximal ends have large lateral articular facets, they do not have the extreme overlap which is characteristic of the Felidae.

The proximal articular surface of metacarpal III is smooth with a slight groove on the dorsal side, and slopes down toward metacarpal II, making an

angle of 75° with the long axis. Immediately distal to this articular surface, on the dorsal side, lies a deep pit for the insertion of a ligament. Another pit is located near the proximal end, distal to the volarad surface, for articulation with metacarpal II. The shaft is slightly convex dorsally in its long diameter. Near its distal end are two very large lateral eminences for attachment of ligaments, a catlike feature. The dorsal side of the distal articular surface presents a surface which is more nearly hemispherical than hemicylindrical, another catlike character. Although the distal keel is strong, it is not so long and narrow as it is in either *Felis* or *Canis*.

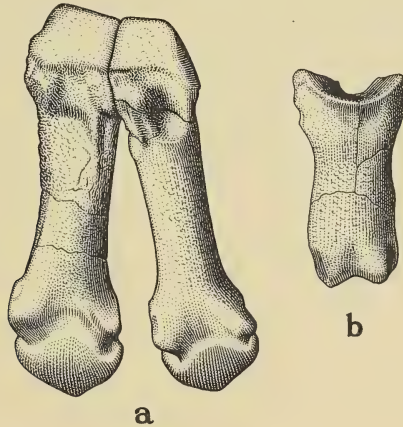


Fig. 3. *Amphicyon?* sp. a, metacarpals III and IV, no. 767, front view; b, phalanx, no. 777, front view. $\times 0.5$.

Calif. Inst. Tech. Vert. Pale. Coll.
Upper Miocene, Tonopah, Nevada

In metacarpal IV the proximal articular surface is smooth and slopes toward metacarpal III. The dorsal articular facet for metacarpal III is flat, in contrast with the slight projection of the surface in *Canis* and the very strong projection in *Felis*. The entire proximal half of the volar side of metacarpal IV is covered by an upraised, wide, flat, rough area for attachment of a ligament. The shaft is straight, not curved as in *Felis*. The distal end resembles that of metacarpal III.

The proximal end of the phalanx presents a deep, smooth, hemispherical cup. The wide, flattened shaft is dorsally convex. Deep lateral pits for insertion of ligaments lie on either side of the broad distal end.

Measurements (in millimeters) of foot elements of Amphicyon? sp.

	AP, anteroposterior diameter		
	Tr, transverse diameter		
	Metacarpals, no. 767		Phalanx, no. 777
	III	IV	
Length	97	98.5	54
Proximal end, AP	36.5	32.5	28
Proximal end, Tr	21.5	27.0	19.5
Distal end, AP	22.7	23.5	14.3
Distal end, Tr	25.8	26.5	21.8
Least dimension of shaft, AP . . .	13.9	14.5	9.8
Least dimension of shaft, Tr . . .	15.0	15.8	17.5

Relationships. Although the foot structure of *Amphicyon* is at present unknown (Matthew, 1924, p. 115), it is believed that these elements from Tonopah are of that genus. The material is not strictly comparable with the metapodials described by Schlosser (1899) as *Amphicyon*. The latter metapodials, from Eckington near Ulm, as Matthew has already noted, "belong to a much smaller animal, very different in foot proportions."

A series of metapodials found in definite association with skull and dentition of *Amphicyon* from Pawnee Creek is in the collections of the U.C. Museum of Paleontology. These Pawnee Creek metapodials are almost identical with C.I.T. no. 767.

MUSTELIDAE

Part of an upper dentition, two mandibular fragments, and several individual teeth clearly belong to mustelids. The minimum mustelid population within the one species which occurs in the Tonopah fauna consists of three individuals, a young adult and two adults of more advanced age.

Brachypsalis pachycephalus Cope

(Plate 3, figures 5, 5a, 7, 7a)

An almost complete maxillary, C.I.T. no. 1231 (pl. 3, figs. 5, 5a), with P¹ to P⁴ in place, a loose M¹, two loose P⁴'s; a ramus, C.I.T. no. 1230 (pl. 3, figs. 7, 7a), with worn C, and P₃-M₂; another partially preserved ramus, C.I.T. no. 778, and individual canine teeth are believed to represent this species.

Skull. The maxillary is short and high. The anterior rim of the orbit lies above the anterior root of P⁴. The lachrymal foramen is large and round. The infraorbital foramen opens over the middle of P³. The malar forms a very massive zygomatic arch. In C.I.T. no. 1231, the least depth of malar below orbit is 13.0 mm.; least distance from rim of infraorbital foramen to orbital rim, 11.8 mm. Corresponding measurements in A.M.N.H. no. 8338, 11.8 and 12.7 mm.

Mandible. The short, heavy mandible deepens posteriorly. Three small mental foramina lie in a horizontal line below the region between P₃ and C. The masseteric fossa reaches forward to a point below the anterior end of M₂.

Upper dentition. Alveoli show that the incisors were large. The upper canines are relatively very large, with short crown and very massive root. The crown is grooved anteriorly from wear against the lower canines. P¹ is a small single-rooted, peglike tooth.

P² and P³ are fairly short and wide and are so worn that the original characters of their cusps are difficult to determine. P² was set slightly diagonal. P³ may have had a small heel cusp.

P⁴ is likewise short and wide. The very large protocone projects strongly forward and inward. A small parastyle is present. A low cingulum lies along the posterior internal base of the metacone. Although the shear of the unworn tooth appears high, the tooth wears to a low cutting edge.

M¹, which has been referred to this species, is characterized by a small paracone, a still smaller metacone, a large ridgelike protocone, almost no sign of metaconule, perhaps because of wear, a parastyle crest, a metastyle crest, and, most important of all, a very strong anterointernal flange which makes the heel of the tooth wider than the outer edge. There is no indication in the specimens available of an alveolus for M².

Lower dentition. The canines are comparable in size with those in the upper dentition. P₁ probably was present in the young animal. From its alveolus P₂ appears to be single-rooted, although the two roots may have been closely appressed.

P₃ and P₄ are rather short and wide like the upper premolars, and have lost all other characters because of wear. A shattered P₄ in specimen C.I.T. no. 778 suggests that there was a posterior accessory cusp on the crown of this tooth.

M₁ is also short and wide, and is characterized by a very strong metaconid and a short heel with a small entoconid crest rather than an entoconid cusp; the surface is worn to a low angle of shear. M₂ is small and almost round in outline, and has a very short basined heel.

Comparative measurements (in millimeters) of dentition of Brachypsalis

1a, b. *B. pachycephalus*, Tonopah. a, C.I.T. no. 1231; b, no. 1230.

2a. *B. ? hyaenoides*, Republican River, A.M.N.H. no. 8338. 2b, *B. pachycephalus*, Upper Miocene, Niobrara, A.M.N.H. no. 8544.

3a, b. *B. matutinus*, Lower Sheep Creek, A.M.N.H. no. 18921.

4a, b. *B. modicus*, Lower Snake Creek. a, A.M.N.H. no. 17210; b, no. 17209.

5a, b. *B. pristinus*, Upper Snake Creek. a, A.M.N.H. no. 18268; b, no. 18922.

Upper dentition:	1a	2a	3a	4a	5a
Length of series P ² -P ⁴	35.0	32.7
C, anteroposterior diameter	13.1
C, transverse diameter	8.8
P ¹ , anteroposterior diameter	2.4
P ¹ , transverse diameter	2.3
P ² , anteroposterior diameter	7.3	7.0
P ² , transverse diameter	5.0	4.6
P ³ , anteroposterior diameter	9.3	8.8
P ³ , transverse diameter	6.5	5.8

Continued on next page

Comparative measurements - Continued

Upper dentition - continued:	1a	2a	3a	4a	5a
P ⁴ , internal anteroposterior diameter . . .	15.4	14.1	13.9	15.5	16.7
P ⁴ , greatest transverse diameter	10.6	10.0	9.0	11.0	12.8a
M ¹ , greatest transverse diameter	12.5	13.0	12.4	14.4	14.3
M ¹ , width of heel	8.0	7.8	6.5	8.0	10.0
Lower dentition:	1b	2b	3b	4b	5b
Depth of jaw at M ₂ -M ₃	23.2	25.3	20.0	18.9
Length of series C-M ₂	64.0	62.4
C, anteroposterior diameter	11.0	10.7
C, transverse diameter	7.6	8.0
P ₃ , anteroposterior diameter	8.0	8.4
P ₃ , transverse diameter	5.0	5.8
P ₄ , anteroposterior diameter	11.0	8.3	10.2	9.6
P ₄ , transverse diameter	6.9	5.7	6.5	5.2
M ₁ , anteroposterior diameter	14.0	14.4a	12.7	15.7a	17.5
M ₁ , transverse diameter	7.5	7.8a	5.6	7.5	8.8
M ₂ , anteroposterior diameter	7.1	6.4
M ₂ , transverse diameter	6.2	4.6

a, approximate.

Relationships. The form and construction of the teeth, especially P⁴ and M¹, reveal the affinities of C.I.T. nos. 1230 and 1231 with the *Paroligobunis-Brachypsalis* group of mustelids (Matthew, 1924, p. 129).

Brachypsalis modicus Matthew (1918, figs. 4, 5) from the Lower Snake Creek approximates C.I.T. no. 1231 very closely in size. The protocone of P⁴ in C.I.T. no. 1231 projects farther forward than in A.M.N.H. no. 17210. This projection is more apparent than real, however, because the parastyle in P⁴ of C.I.T. no. 1231 is entirely worn away and this has shortened in appearance the anteroposterior diameter taken through the outer section of the tooth. M¹ of C.I.T. no. 1231 has a smaller paracone than A.M.N.H. 17210. The advanced age of C.I.T. no. 1230 partly accounts for such differences in the lower jaw as loss of P₁, constriction of alveolus of P₂, and increased heaviness and depth of jaw. For the most part the lower dentitions are similar.

Brachypsalis pristinus (Matthew, 1904, 1924) differs from C.I.T. no. 1231 in its much larger P⁴ with no parastyle. M¹ is also much larger and bears a strong posterior heel crest. The lower jaw of this Upper Snake Creek species is not so deep as in C.I.T. no. 1230, but M₁ bulks larger, especially in the heel region. P₄ of A.M.N.H. no. 18922 is distinctly more slender than P₄ of the Tonopah form.

Brachypsalis matutinus Matthew (1924) of the Lower Sheep Creek is much smaller all around, and has a more elongate M₂.

Brachypsalis obliquidens Sinclair (1915) from the Upper Snake Creek is characterized by large teeth, greatly crowded in the lower jaw so that P₂ and P₃ are set obliquely in the jaw.

Brachypsalis marshalli Martin (1928) from Edson, Kansas, differs in its larger size, and in its relatively shorter, wider teeth.

Brachypsalis angustidens Hall (1930a) from the Kern River Pliocene is much smaller than the Tonopah species.

The skull fragment with superior dentition, A.M.N.H. no. 8338, the type of *Aelurodon hyaenoides* Cope from Driftwood Creek, Nebraska (Cope, 1881, p. 388; 1883, p. 244, fig. 11c; Cope and Matthew, 1915, pl. 119a, fig. 5), was considered by Matthew (1918, pp. 195-196) to represent *B. pachycephalus*. This form, though slightly smaller than C.I.T. no. 1231, resembles it closely in character of the dentition. In both forms P^1 is a peg, P^2 is set slightly oblique, and the protocone of P^4 projects rather far forward. M^1 , though similarly constructed, is a little larger transversely in A.M.N.H. no. 8338.

The type of *B. pachycephalus* Cope (1890), A.M.N.H. no. 8544 from the Loup Fork Upper Miocene, resembles C.I.T. no. 1230 in length of tooth row and apparently in size of lower carnassial. Unfortunately, the type is fragmentary and the teeth are either absent or, as in the case of M_1 , badly broken. The jaw of the type is slightly deeper and more massive.

Although the type material is poorly preserved, the referred specimen, A.M.N.H. no. 8338, still shows some distinguishing characteristics. If this reference by Matthew is correct, then the relationships of the Tonopah species are with *B. pachycephalus* Cope.

An undescribed maxillary dentition, U.C. no. 35447 from Barstow, closely resembles C.I.T. no. 1231, although P^2 - P^4 are slightly more massive in the former than in the latter specimen.

FELIDAE

The cats appear to be represented in the Tonopah collection by remains of at least five individuals. The skull and lower jaw material was described in detail by Stock (1934). Though the specimens varied somewhat in size and slightly in characters, Stock referred all of them to *Pseudaelurus intrepidus* Leidy.

Pseudaelurus intrepidus Leidy

Relationships. Stock has pointed out that C.I.T. no. 791 is closely similar to the Old World *Pseudaelurus*, and differs from *Metailurus* Zdansky (1924) in premolar dental formula and in having an alisphenoid canal.

Pseudaelurus marshi Thorpe (1922) agrees closely with C.I.T. no. 1233 in size, but differs in a number of minor respects (see Stock, 1934). Except for the smaller size of the lower jaw material, the Tonopah felid agrees closely in all respects with the type *P. intrepidus*.

A part of a lower jaw without teeth, U.C. no. 21516, from the Barstow beds, is larger, deeper, and heavier than C.I.T. no. 1233. Fragmentary material from the Avawatz Mountains, C.I.T. no. 2309, represents a type larger than C.I.T. no. 1233 in all measurements, with more crowded teeth, and with a smaller heel cusp in M_1 . Specimens from the Cedar Mountain region (Merriam, 1916a) and from Thousand Creek (Merriam and Stock, 1928) are too fragmentary to be of any diagnostic value.

EQUIDAE

Remains of the Equidae comprise the bulk of the fossil collection from Tonopah. Isolated teeth and foot bones are preserved in greatest abundance. Maxillary and mandibular tooth rows make up a considerable part of the collection, but there are no complete skulls. Curiously, only a few poorly preserved vertebrae were found.

All the equid material may be divided into two distinct groups, the hypohippine and the merychippine. A population count based on astragali and teeth indicates a minimum of approximately 10 adult and 2 young hypohippine individuals, and 100 adult and 10 young of *Merychippus*.

All the specimens referable to *Hypohippus* appear to fall into a single species.

The merychippine material, although extremely abundant, shows surprisingly little variation. Hence, the specific and subspecific differentiation which was encountered in the Sheep Creek, Pawnee Creek, Snake Creek, and Barstow faunas contrasts with a stability of type in the Tonopah assemblage.

Hypohippus near *affinis* (Leidy)

(Plate 5; plate 6; plate 8, figures 1, 1a; plate 9, figures 1, 1a)

Skull. The infraorbital foramen in maxillary C.I.T. no. 685 lies directly above the anterior part of P^4 . The diastema between I^3 and C ranges from 12 to 15 mm. in length, and the diastema between C and P^1 falls between 27 and 22 mm. in length.

Mandible. A single specimen representing the symphyseal region indicates that the diastema between C and P_2 approximates 42 mm. in length. The mental foramen is located below the posterior part of the diastema. In C.I.T. no. 680, the anteroposterior diameter of the symphysis measured on inferior border from notch to base of crown of I_1 is 65.6 mm.; least width of symphyseal region, 24.0 mm.; least depth of symphyseal region, 22.5 mm.; depth normal to alveolar border anterior to P_2 , approx. 35 mm. In C.I.T. no. 1881, the depth normal to the alveolar border anterior to M_1 is 46 mm.

Upper permanent dentition. The collections of the California Institute include two almost complete upper dental series, nos. 1404 and 1401 (pl. 5, figs. 1, 2), as well as a number of shorter series, nos. 1238, 1239, 1879, and 2860 (pl. 6, figs. 1, 1a).

The incisors are large, short-crowned, and deeply cupped, but uncemented. A strong break occurs between the thickly enameled crown and the root. The large, short canine has a rounded exterior surface, and a strong median ridge on the inner surface.

P^1 is a relatively large, short-crowned, double-rooted tooth. It appears to be cupped on the occlusal surface, and is suboval in outline.

In striking contrast with those of *Merychippus*, the molariform teeth are by no means subequal in size. The teeth of the premolar row increase steadily in

size from P^2 to P^4 , the latter being the largest of the cheek teeth. The molar teeth decrease rapidly in size from M^1 , which is almost as large as P^4 , to M^3 , by far the smallest of all the cheek teeth.

The large protocone displays a characteristic subconical shape with anterior border flattened, and is larger than the hypocone. A strong cingulum anterior to the protocone usually disappears on the median border of the base of the protocone. In teeth of one premolar series, C.I.T. no. 1879, the cingulum continues across the median border of the base of the protocone. In P^3 , P^4 , and M^3 the internal basal border of the protocone lies lingual to that of the hypocone.

Normally the protoloph remains separate from the ectoloph. Generally speaking, the anterior premolars show greatest separation of protoloph from ectoloph. The extent of this separation decreases progressively toward the posterior molars. With increased wear the protoloph tends to become attached to the ectoloph. Such attachment has been observed in several specimens of M^1 , but in only one example of P^4 . In a few cases the protocone is separate from the protoconule, but the two cusps are usually joined together.

The hypocone is slightly smaller than the protocone and is not so perfectly conical in shape. A small cingulum may be present at the medial end of the valley between protocone and hypocone, usually on P^2 , sometimes on P^3 , never on the other teeth. In well worn teeth the hypocone and hypostyle are connected.

The metaloph is attached to the ectoloph in almost all permanent teeth of *Hypohippus* in the collection. P^2 in C.I.T. no. 1239 forms a single exception. The transverse crest which makes the connection curves anteriorly from the hypocone, then swings back to join the ectoloph at a point opposite the mesostyle.

The large hypostyle is generally cupped posteriorly. With wear, the cup or infold disappears. The hypostyle generally remains discrete, though with wear it does become connected with the hypocone. A moderately strong cingulum borders the tooth between the hypostyle and the hypocone. In one premolar series, C.I.T. no. 1879, the cingulum actually traverses the base of the hypocone and is continuous with the cingulum of the protocone.

A narrow ridge joins the hypostyle with the metastyle. This tenuous connection is completed at a later stage of wear than is that between hypocone and ectoloph, but is usually earlier than the connection between protocone and ectoloph.

Crochets reaching forward from the metaconule appear on several third molars. The fossettes are rarely closed, and then only when the tooth has been greatly worn. In some specimens a few plications have been observed on the metaloph in the prefossette and postfossette areas.

Strong, massive external styles characterize the teeth. Cement is completely absent. The occlusal surface of the permanent upper cheek teeth varies in

shape. It may be square, or rectangular with the transverse width much greater than the anteroposterior.

The following measurements (in millimeters) give the maximum heights of the low, strongly curved crowns: C.I.T. no. 1879, P^2 , 17.0 mm.; P^3 , est. 18.5 mm.; P^4 , 19.0 mm. C.I.T. no. 1239, M^1 , 17.2 mm.; M^2 , 17.7 mm. C.I.T. no. 1404, M^3 , 16.5 mm.

Upper deciduous dentition. Only two teeth, both representing Dm^2 , occur in the collection, C.I.T. nos. 2845 and 2846 (pl. 6, figs. 2, 3). In these the protoloph is not connected with the ectoloph, and in C.I.T. no. 2845 the protocone is separated from the protoconule. The cingulum, though well developed along the anterior side of the teeth, is absent on the inner base of both protocone and hypocone.

The separation of metaloph from ectoloph forms an important diagnostic character. A small transverse ridge points inward from the ectoloph at the posterior end of the paracone crescent. The outer end of the metaloph ridge terminates just anterior to the transverse ridge of the ectoloph. The two ridges overlap and come very close to each other, but they are not joined together except perhaps at the very base.

The hypostyle is much more suppressed than in permanent teeth. The shape of the occlusal surface of Dm^2 is like that of P^2 : anteroposterior diameter along outer border, 29 mm.; greatest transverse diameter, 26.5 mm. The crown height in Dm^2 is 14 to 15 mm.

Lower permanent dentition. The incisors, C.I.T. no. 680, are long-rooted, short-crowned, and not so procumbent as are the merychippine lower incisors. A strong dividing line distinguishes the upraised, thickly enameled crown from the root. Very shallow uncemented cups occur near the posterior border of the occlusal surface.

P_1 , C.I.T. no. 2847 (pl. 6, fig. 4), is a small, single-rooted tooth which from root to crown is concave anteriorly. The crown is laterally compressed, with a faint anterior tubercle and a large posterior tubercle.

The collections of the California Institute include only two well preserved series of lower molariform teeth, nos. 1880 and 1881 (pl. 5, figs. 3, 4). As with the upper cheek teeth, P_4 is the largest and the remaining teeth are successively smaller in either direction from it.

In the molariform teeth the metaconid-metastylid column bears no pronounced gutter on its inner wall. There is sometimes a very slight groove near the summit of the column. With wear the column increases very rapidly in anteroposterior diameter.

The entostylid is distinct on unworn teeth. The posterior lobe of M_3 is relatively small. The triangular entoconid becomes square with wear. The external walls of the protoconid and hypoconid display a strongly curved, finely fluted enamel surface. A very deep valley lies between the protoconid and hypoconid. No cement is present on the teeth.

A strong cingulum, which rises high on the anterior border of the tooth,

skirts the external basal border of the protoconid. A second cingulum originates in the protoconid-hypoconid valley, skirts the external basal border of the hypoconid, then rises sharply to the posterior border of the tooth.

The occlusal surfaces are relatively short and wide. Ratios of antero-posterior diameter to transverse diameter: P_3 , 1.20-1.40; P_4 , 1.15-1.36; M_1 , 1.25-1.30; M_2 , 1.23-1.39; M_3 , 1.60-1.70.

The maximum crown height for all the lower molariform teeth is approximately 20 mm.

Lower deciduous dentition. The milk tooth, Dm_3 or Dm_4 , C.I.T. no. 2848 (pl. 6, fig. 6), resembles the permanent dentition in almost every respect. The height of the crown is less and the entostylid is stronger than in permanent teeth. Anteroposterior diameter, 28 mm.; transverse diameter, 18 mm.; crown height, 12 mm.

Measurements (in millimeters) of dentition of Hypohippus near affinis

AP, anteroposterior diameter

Upper dentition:	C.I.T. no. 1404	C.I.T. no. 1401
Length of series P^1-M^3	164	145
Length of series P^1-P^4	92	82
Length of series M^1-M^3	72	63
P^1 , anteroposterior diameter	14.2	16.7
P^1 , greatest transverse diameter	8.2	10.4
P^2 , AP along outer border	30.0	26.5
P^2 , AP protoconule-hypostyle	24.0	20.0
P^2 , greatest transverse diameter	27.4	26.4
P^3 , AP along outer border	29.2	25.0
P^3 , AP protoconule-hypostyle	26.0	23.0
P^3 , greatest transverse diameter	32.5	29.8
P^4 , AP along outer border	30.5	25.5a
P^4 , AP protoconule-hypostyle	27.2	23.2
P^4 , greatest transverse diameter	33.8	32.5a
M^1 , AP along outer border	28.5	24.9
M^1 , AP protoconule-hypostyle	25.0	22.1
M^1 , greatest transverse diameter	32.5	30.5
M^2 , AP along outer border	28.8	23.0
M^2 , AP protoconule-hypostyle	24.2	21.0
M^2 , greatest transverse diameter	31.4	27.5
M^3 , AP along outer border	23.2	20.4
M^3 , AP protoconule-hypostyle	22.5	19.0
M^3 , greatest transverse diameter	25.4	25.0
I^1 , greatest diameter	14.4
I^1 , least diameter	11.6
I^2 , greatest diameter	12.8	11.6
I^2 , least diameter	10.3	8.5
I^3 , greatest diameter	9.7	9.2
I^3 , least diameter	7.9	5.4
C, greatest diameter	11.4
C, least diameter	8.7
Diastema, I^3-C	18e	14
Diastema, $C-P^1$	23a	28a

a, approximate.

e, estimated.

Continued on next page

Measurements - Continued

Lower dentition:	No. 1880	No. 1881	No. 2847
Length of series P ₂ -M ₃	148
Length of series P ₂ -P ₄	74.5
Length of series M ₁ -M ₃	73.5
P ₁ , anteroposterior diameter	9.1
P ₁ , transverse diameter	5.0
P ₂ , anteroposterior diameter	24.0	23.6
P ₂ , transverse diameter	16.3	17.3
P ₃ , anteroposterior diameter	24.2	23.2
P ₃ , transverse diameter	17.5	19.2
P ₄ , anteroposterior diameter	24.8	24.0
P ₄ , transverse diameter	19.5	20.9
M ₁ , anteroposterior diameter	23.8	23.9
M ₁ , transverse diameter	18.4	19.0
M ₂ , anteroposterior diameter	24.0	22.5
M ₂ , transverse diameter	17.3	18.3
M ₃ , anteroposterior diameter	23.5	25.5
M ₃ , transverse diameter	14.7	15.0
No. 680			
I ₁ , greatest diameter			9.4
I ₁ , least diameter			9.0
I ₂ , greatest diameter			9.0
I ₂ , least diameter			8.3

Relationships. *Hypohippus nevadensis* Merriam (1913b) of the neighboring Esmeralda fauna presents several characters which find analogies in *H. near affinis* from Tonopah. The former species was first described from the Esmeralda (U.C. locality 1980) near Cedar Mountain, Nevada. Further material from Fish Lake Valley, Nevada, was assigned to this species by Stock (1926). A detailed comparison between the Tonopah species and *H. nevadensis* reveals a similarity in characters, but a discrepancy in size. Unfortunately for comparison, the material of the type *H. nevadensis* consists of deciduous upper cheek teeth and M¹. Dm² from Tonopah is much smaller than Merriam's type, U.C. no. 21056, and somewhat smaller than the specimen from Fish Lake Valley, U.C. no. 27116. The largest M¹ in the Tonopah collection is much smaller in all dimensions including height of crown than M¹ of U.C. no. 27116. The deciduous teeth of *H. near affinis* resemble those of the Cedar Mountain species in separation of metaloph from ectoloph, in which respect also they differ from the Fish Lake Valley form. Whereas the metaloph and ectoloph are separate in M¹ of U.C. no. 27116 from Fish Lake Valley, these crests are joined in all permanent cheek teeth from Tonopah except P², C.I.T. no. 1239. A crochet is present in Dm² and Dm³ of U.C. no. 27116, but is weak in Dm⁴ and absent in M¹. In the Tonopah collection only one tooth, an M³, bears a crochet. A cingulum traversing the entire inner border of the upper cheek teeth may be present or absent in the material from the three Nevadan localities.

Lower teeth of *H. near affinis* resemble those from Fish Lake Valley in

every respect except size. The latter lower teeth are larger by about the same amount as are the upper teeth.

Limb elements of the Tonopah species closely approximate in size those of U.C. no. 21056 from Cedar Mountain. It must be remembered, however, that the limb elements of *H. near affinis* are those of a large adult, whereas U.C. no. 21056 represents a very young individual.

In summary, the major difference between the Tonopah form and *Hypohippus nevadensis* from Cedar Mountain and Fish Lake Valley is one of size. The latter averages one-sixth to one-eighth larger lineally than the former. In *H. nevadensis* the importance of separation of metaloph from ectoloph and the development of a crochet may be overestimated. Merriam (1913b) based the new subgenus *Drymohippus* on this separation of lophs. After reviewing the Fish Lake Valley material, Stock (1926, p. 64) commented: "If the form from the Fish Lake Valley region has been correctly assigned to Merriam's species, this character appears to be subject to individual variation and cannot, therefore, be considered as distinguishing *Drymohippus*. Likewise, the development of a crochet in the milk teeth would not then offer a constant character distinguishing *Drymohippus* from other members of the *Hypohippus* group." (See also McGrew, 1938, p. 314.) In the figure of *Hypohippus equinus* Scott (1895), on P² the metaloph is apparently separate from the ectoloph. The Tonopah material, with metaloph and ectoloph joined in all except two milk teeth and in P², bears out the contention that such variations may be common to many hypohippines.

Hypohippus osborni Gidley (1907, p. 930) is considerably smaller than the largest *H. near affinis*, although only slightly smaller than the smallest individuals referable to this species.

Hypohippus near affinis from Tonopah falls short of the type *H. affinis* (Leidy) in size. Material from Big Spring Canyon, A.M.N.H. no. 10834, which was assigned to the type *H. affinis* by Gidley (1906, p. 135), shows that the lower teeth of *H. affinis* are somewhat larger than those of the Tonopah form.

A molar series, P³-M³, U.C. no. 32019, from the Niobrara River U.C. locality Little Beaver A V336 is smaller than the corresponding teeth from Tonopah. In this specimen there is a firmer connection between metaloph and ectoloph, and a small conical cuspule is present at the lingual end of the protocone-hypocone valley of each tooth. A small crochet is developed in P⁴. The protocone and the protoconule show a tendency to remain separate in the premolars. In this latter character and in size, the Niobrara River specimen appears a little more primitive than *H. near affinis*, whereas on the basis of metaloph-ectoloph connection the Tonopah form may be slightly more primitive. *Hypohippus near affinis* is interpreted to be more advanced but situated on a closely allied side branch which retained the primitive separation of metaloph and ectoloph.

Well preserved series of upper and lower permanent teeth and upper milk

teeth of *Hypohippus affinis* in the Burge fauna have been illustrated by McGrew (1938). These teeth agree closely in size with those of *H. near affinis*. A partially erupted M^1 in U.C. no. 28842 indicates that the Burge form is much higher-crowned. The tooth pattern of U.C. no. 28840 differs in the presence of a crochet on the metaloph, in better connection of metaloph and ectoloph, and in the development in the last two molars of a small conical cuspule at the lingual end of the protocone-hypocone valley. The lower molars U.C. no. 28840 are similar in pattern to those of *H. near affinis*, but are somewhat higher-crowned, and have a larger posterior lobe in M_3 .

Known material of *Hypohippus* from Barstow is too fragmentary to afford any comparisons of value. On the basis of broken lower teeth U.C. nos. 21215 and 35421, the Barstow form appears larger than *H. near affinis*, yet in all probability it, too, lies near that species.

Hypohippus near affinis from Tonopah may have been ancestral to *Hypohippus nevadensis*. The former type represents a stage of development which is slightly more primitive than that shown in *H. affinis* from the Burge of Gordon Creek, and is more advanced than that of *H. cf. osborni* from the Niobrara River of U.C. locality Little Beaver A V336.

Merychippus calamarius (Cope)

(Plate 7; plate 8, figures 2, 2a; plate 9, figures 2, 2a; text figures 4, 5)

Skull. Only a few minor characters are determinable from the sparse and fragmentary skull material. In C.I.T. no. 2839 the infraorbital foramen lies directly above the posterior part of P^3 and the anterior border of P^4 . The anterior border of the orbit reaches as far forward as the plane of contact between M^3 and M^2 . The diastema between I^3 and C ranges from 19 to 24 mm. in length, and the diastema between C and P^1 varies inversely in length from 32 to 26 mm.

Mandible. Although symphyseal sections and horizontal parts of rami were preserved in considerable abundance, no material is available to illustrate the region of the angle and the ascending ramus. In C.I.T. no. 2836 (pl. 7, fig. 5), the canine is immediately posterior to I_3 . The diastema between C and P_2 is from 43 to 49 mm. long. The mental foramen is located halfway between C and P_2 . In young animals the tooth size and the diastemal length is the same as in adults. Growth in the mandible takes place by deepening of the jaw from 40 mm., just posterior to Dm_4 in a young foal, C.I.T. no. 2833, to 50 mm., between P_4 and M_1 in a young adult, C.I.T. no. 2834. The mandible is also thickened by growth. The greatest increase in size and in length, however, takes place in the molar region, as the ascending ramus is pushed back to make room for the molar teeth.

Most of these characters are well illustrated in mandibles C.I.T. nos. 656, 678, and 2834 (pl. 7, figs. 2, 2a, 7, 8).

Measurements (in millimeters) of mandible of Merychippus calamarius

	C.I.T. no. 2834 (young adult)	C.I.T. no. 678 (youth)	C.I.T. no. 656 (foal)
Anteroposterior diameter of symphysis measured on inferior border from			
crotch to root of I_1	50a	49	40
Least width of symphyseal region	28.4	23.0	19.0
Least depth of symphyseal region	22.0	20.4	16.5
Depth normal to alveolar border			
anterior to P_2	32.9	31.0	21a
Depth normal to alveolar border			
anterior to M_1	51.4	43e	22e

a, approximate.

e, estimated.

Tooth wear. Advanced stages of wear efface details of the enamel pattern and destroy the original proportions of the occlusal surface. Hence, well worn teeth tend to lose many of the characters on which specific determinations are made. For this reason, in the following discussion, all remarks apply to teeth which are approximately one-third worn except as otherwise indicated. Teeth which are unworn to one-third worn are designated as *unworn*, teeth which are more than one-third worn are termed *worn*. The state of wear of any given tooth was determined by comparing the height of the crown with the maximum crown height for that tooth.

Upper permanent dentition. The limited extremes of variation in the abundantly represented merychippine form are illustrated by C.I.T. nos. 2840, 2841, 1311, 669, and 2839 (fig. 4, a-e, respectively). The incisors are strongly curved and relatively long-crowned with no sharp break between crown and root. The enamel gradually becomes thinner and disappears toward the root. In each incisor the grinding surface is deeply cupped and the enamel infold is filled with cement.

The upper canine is a strongly curved, peglike tooth. Occasionally the piercing end of the tooth, instead of being circular in cross section, is somewhat flattened on the lingual side of the anterior and posterior edges, so that the tooth appears as a small curved blade supported by a column on the lingual side.

P^1 is a small, short-crowned, double-rooted tooth located immediately anterior to P^2 . It is generally well worn at an early stage and is often lost soon after maturity. Because the angle of the surface of wear on this tooth may vary greatly, its enamel pattern appears in a number of diverse forms. Basically it consists of a prominent outer border, a strong metaconule, and a partially enclosed prefossette opening toward the front.

Separation of the protocone from the protoconule occurs in almost 90 per cent of the unworn molariform teeth. In only 14 per cent of the unworn teeth is the protocone rounded or oval. In the rest it has a spur projecting toward the protoconule. The protocone is generally inflated, although

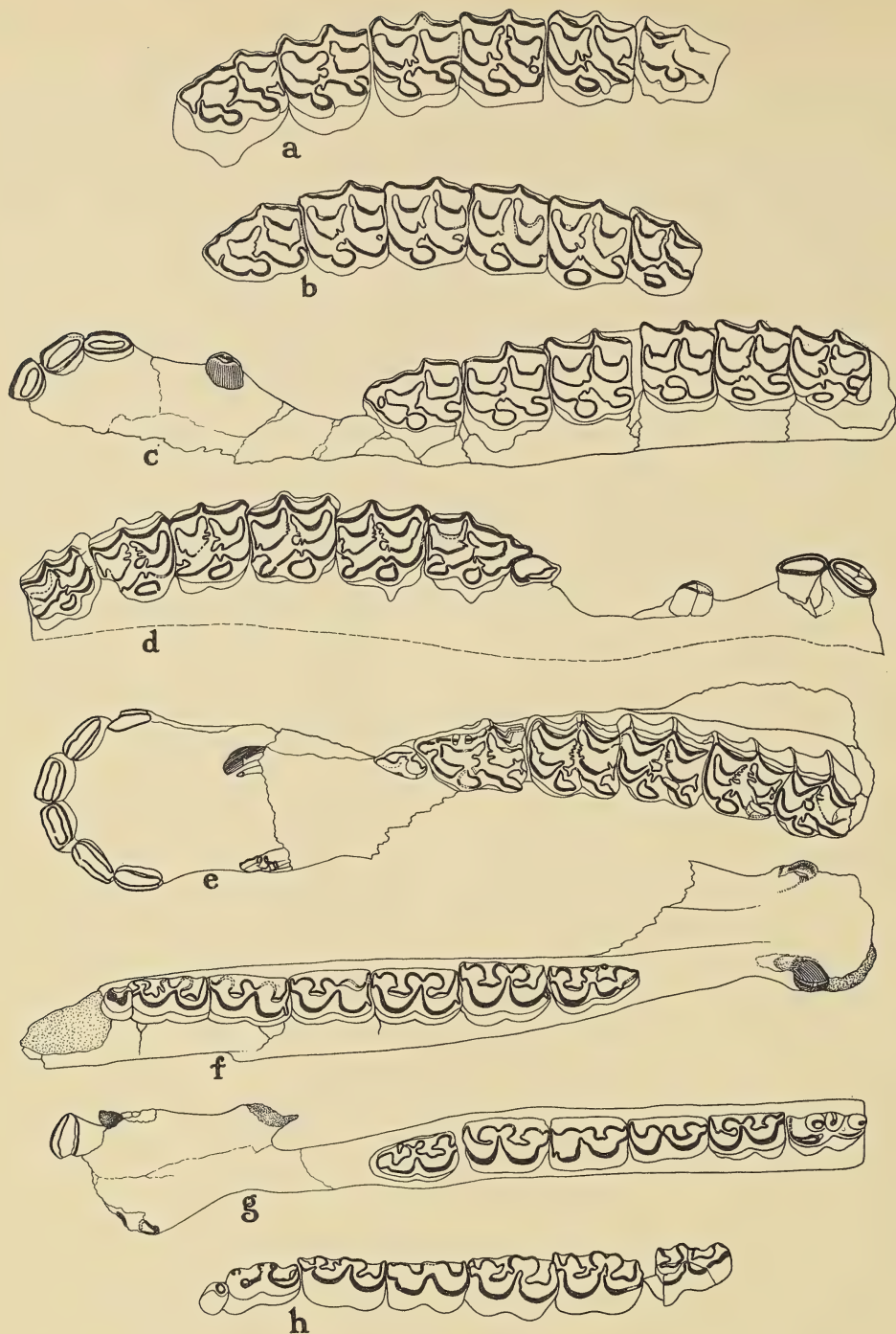


Fig. 4. *Merychippus calamarius* (Cope). Referred specimens, showing variation in enamel pattern. a, no. 2840, moderately worn; b, no. 2841, moderately worn; c, no. 1311, moderately worn; d, no. 669, slightly worn; e, no. 2839, unworn; f, no. 2834, moderately worn; g, no. 678, slightly worn; h, no. 2842, slightly worn. All figures $\times 0.5$.

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it may be flattened on the lingual side. Indented protocones rarely occur. The long axis is oriented for the most part anteroposteriorly. The protocone usually lies lingual to the posterior half of the prefossette. In some cases, however, and always in M^3 , it is more posterior, extending back to a position lingual to the metaconule. The protocone is always larger, more inflated, and more lingual in position than the hypocone.

The hypocone is practically always united with the metaconule. It is generally flattened, although it may be rounded in some specimens. The long axis of the hypocone is almost never oriented anteroposteriorly.

The pli caballin is generally single and acutely pointed, sometimes single and rounded, and rarely bifid or double. The hypostyle sometimes has no plications, but commonly has a single acute plication and rarely a double one.

The fossettes are usually closed in all teeth except P^2 . The various plications range in number from none to quadruple folds. On the whole, the fossette borders would be called moderately to highly complex for a merychippine form. There appears to be a direct correlation between protocone separation and degree of complexity of the enamel pattern. The more complete the separation, the more complex the pattern.

The external styles are strong. Moderately heavy to heavy cement covers most of the teeth.

In M^1 and M^2 the ratios between anteroposterior and transverse diameters vary from 1.18-1.10 in absolutely unworn teeth to 0.90-0.76 in very worn teeth. Because of the cement covering on most of the teeth, inaccuracies enter into the measurements of the transverse diameters (Bode, 1931, p. 122).

The crowns of the molariform teeth are strongly curved (C.I.T. no. 2861, pl. 7, fig. 4a). In unworn teeth the radius of curvature of the external styles generally falls between 40 and 50 mm. The radius of curvature of the lingual side of the protocone ranges between 12 and 18 mm. In unworn upper teeth the maximum crown height is greater than in any merychippine species previously recorded (C.I.T. no. 2861, pl. 7, fig. 4).

Measurements (in millimeters) of crown heights of upper teeth

	A	B
P^1	9	...
P^2	35	37
P^3	39	41
P^4	42	45
M^1	40a	43a
M^2	44	47
M^3	36	41

a, approximate.

These measurements were taken of separate unworn teeth and of unerupted teeth in maxillary batteries. In column A, crown height is considered to be the shortest distance from root to grinding surface taken just anterior to the mesostyle, with the notch between the external roots furnishing one

measuring point and the indentation on the external wall of the tooth between paracone and metacone furnishing the other measuring point. The measurements in column B were taken by the method used by Bode in compiling data for a table comparing the crown heights of merychippine forms from Mascall, Coalinga, Barstow, and Tonopah (Bode, 1934, p. 56). The measuring points in this case were the base of the anteroexternal root and the tip of the paracone cusp.

Upper deciduous dentition. The incisors are large, deeply cupped teeth without cement. Dm^1 , as it appears in C.I.T. no. 2835, is slightly longer than P^1 . The metaconule is poorly developed, hence the tooth is bladeliike in appearance and shows no tendency toward developing fossettes.

Character for character, the molariform deciduous teeth C.I.T. no. 2843 (pl. 7, figs. 6, 6a) resemble closely the permanent premolars, except for the expected differences between deciduous and permanent teeth. In the molariform deciduous teeth the protocone remains free until the crowns are more than half worn. The fossette borders are a little more complexly plicated than they are in the permanent series. Also in the deciduous teeth the cement varies from a thin film on the outer walls and none in the fossettes to a moderately thick external coating and a thin film in the fossettes. The following maximum crown heights were measured from the roots to the notch between the paracone and metacone cusps: Dm^3 , approx. 16 mm.; Dm^4 , approx. 17 mm.

Lower permanent dentition. A symphyseal section of the jaw with incisors and canines complete, C.I.T. no. 2836 (pl. 7, fig. 5), shows that the lower incisor teeth, like the uppers, are relatively long-crowned and have no sharp break between crown and root. As in the uppers, the grinding surface is characterized by deep cement-filled cups. The lower incisors differ from the upper in their more procumbent position, and their crowns are therefore not so sharply curved.

The lower canine is less curved than the upper. The root is circular in cross section. The piercing end of the tooth is flattened on the buccal as well as on the lingual side along the anterior and posterior edges. This gives the tooth the appearance of a central cone with anterior and posterior flanges.

P_1 , based on a single separate tooth, C.I.T. no. 2837 (pl. 7, fig. 1), is very small, with two rounded roots closely appressed. In an anteroposterior direction the tooth is pinched in where the crown and roots join. The crown is strongly compressed laterally, with sharp anterior and posterior edges.

Variation in the lower molariform teeth is illustrated by C.I.T. nos. 2834, 678, and 2842 (fig. 4, *f-h*, respectively). The stout premolars tend to be a little shorter anteroposteriorly and much wider transversely than the molars. In the molariform teeth the anteroposterior length of the metaconid-metastylid column is relatively great. The values for the ratio metaconid-metastylid length to anteroposterior length for P_3 through M_2 range from 0.35 to 0.53, and the mean value for each of these teeth falls between 0.41 and 0.45.

Measurements (in millimeters) and ratios of measurements

AP, anteroposterior length of tooth.

MCS, anteroposterior length of metaconid-metastylid column.

M/A, ratio of MCS to AP.

	Max. AP	Min. AP	Mean AP	Max. MCS	Min. MCS	Mean MCS	Max. M/A	Min. M/A	Mean M/A
P ₂ (separate)	25.5	21.8	24.0	6.7	5.0	5.9	0.28	0.20	0.243
P ₃ (in place)	24.2	21.4	23.2	11.2	8.5	9.9	0.48	0.35	0.429
P ₃ and P ₄ (separate)	25.0	20.5	22.8	11.8	8.4	10.2	0.53	0.38	0.448
P ₄ (in place)	25.2	20.3	23.1	11.5	8.8	10.3	0.50	0.37	0.444
M ₁ (separate)	25.0	19.3	22.6	10.5	8.0	9.3	0.49	0.36	0.413
M ₂ (separate)	26.4	19.5	22.9	11.0	7.7	9.5	0.46	0.36	0.417
M ₃ (separate)	27.5	24.0	26.1	8.7	6.5	7.7	0.33	0.26	0.294

In P₂ the metaconid occasionally stands as a small separate column half-way between the metastylid and parastylid. In such cases the anteroposterior diameter across the metaconid and metastylid column is much greater than it is when the two are joined into one column, and the mean ratio of metaconid-metastylid length to anteroposterior length becomes 0.36.

The gutter on the inner wall of the metaconid-metastylid column is sharply incised to rounded. Though the gutter disappears with wear, it is always of pronounced depth in unworn teeth. P₂ characteristically has a small gutter and a metastylid which is often more highly developed than the metaconid. In all other teeth the metaconid surpasses the metastylid in size. The posterior lobe of M₃ is greatly extended.

The parastylid swings inward lingual to a plane tangent to the lingual side of the metaconid-metastylid column.

The entoconid may be in any form from triangular (often indented) to rounded to almost rectangular, but is generally rounded and strongly inflated.

The posterior extension of the entostylid, though commonly strong in unworn teeth and especially strong in the molars, varies considerably from one tooth to another. With increased wear the entostylid decreases in size.

The external walls of the protoconid and hypoconid are strongly curved in unworn teeth. One or two unworn teeth and a few worn teeth in the collection show a slight tendency toward flattening of the outer walls of these cusps. The sharp, deep V of the valley between the cusps generally points anteriorly. With wear the valley becomes more shallow and open.

As in the upper dentition, the lower teeth sometimes have little or no cement on the external walls, but most of the teeth would be characterized as moderately to heavily cemented.

The anteroexternal fold is present on more than 75 per cent of the lower teeth. It rarely appears in teeth less than one-fourth or more than three-fourths worn.

As in the upper cheek teeth, the shape of the occlusal surface varies primarily with the stage of wear of the tooth. Measurements on loose unworn teeth and on worn teeth in the jaw yielded the following results:

Ratios of anteroposterior diameter to transverse diameter in lower teeth

	Unworn teeth			Worn teeth
	Minimum	Maximum	Average	Average
P ₂	1.81	2.26	2.01
P ₃ and P ₄ .	1.60	1.98	1.76	1.57
M ₁	1.93	2.50	2.23	1.47
M ₂	2.04	2.60	2.36	1.81
M ₃	2.46	3.27	2.90

The extent of plication of the enamel walls of the lower cheek teeth is very slight, hence the pattern would be termed simple.

On unworn teeth the maximum crown height is greater than in any merychipine previously recorded. In C.I.T. no. 2862 (pl. 7, fig. 3), the crown height of P₁ is 8.5 mm.; P₂, 32 mm.; P₃, 47 mm.; P₄, 47 mm.; M₁, 41 mm.; M₂, 38 mm.; M₃, 38 mm. These measurements were made on loose unworn teeth and on unerupted teeth in the mandible. The measuring points were taken as the notch between the roots on the external side and the notch between the metaconid and metastylid cusps.

Lower deciduous dentition. The incisors are large, deeply cupped, and uncemented. A symphyseal section of a newborn foal, C.I.T. no. 2838, bearing only the first incisors and canines, reveals that D_c is flattened on the inner side. Dm₁, C.I.T. no. 660, left ramus, appears as a small peglike tooth.

In the molariform deciduous teeth C.I.T. no. 656 (pl. 7, figs. 2, 2a), the ratio metaconid-metastylid length to anteroposterior diameter of the tooth is very constant. This constancy probably arises from the shortness of crown, which does not permit much variation with crown height. The ratio metaconid-metastylid length to anteroposterior diameter for Dm₂ ranges from 0.36 to 0.39 mm.; for Dm₃, 0.45 to 0.50 mm.; for Dm₄, 0.42 to 0.45 mm. These ratios for Dm₃ and Dm₄ correspond closely to similar ratios determined for the permanent premolars P₃ and P₄. The ratio for Dm₂ is higher than all ratios for normal P₂, although it is identical with the ratio determined for the second premolars in which the metaconid stands as a separate column from the metastylid.

In Dm₃ and Dm₄ the metaconid-metastylid column has about the same strength as it has in P₃ and P₄. It is normally stronger, however, in Dm₂ than in P₂.

The gutter on the inner wall is sharply incised and of about equal depth for all three deciduous molars, hence the gutter in Dm₂ is relatively much deeper than that in P₂.

As in permanent premolars, the metastylid in Dm₂ is more highly developed than the metaconid, but the reverse is true of Dm₃ and Dm₄. In contrast with the entoconid in permanent teeth, that in milk teeth is triangular to strongly indented. Only after considerable wear does it appear rounded. In Dm₂ and Dm₃ the entostylid is strong and is sharply curved linguallly. In Dm₄ the very strong entostylid projects posteriorly with only a slight inward curvature. The strongly curved external walls show no flattening. The enamel shows a

distinctively finely fluted surface. The very deep valley between protoconid and hypoconid points anteriorly. Though a few of the teeth lack cement almost completely, most of them are thinly coated with it, and some might be termed moderately cemented. The anteroexternal fold is very well developed toward the base of the crown in Dm_3 and Dm_4 . It is slightly to moderately developed in Dm_2 . In approximately two-thirds of the milk teeth in the collection, the external tubercle between protoconid and hypoconid is moderately developed to well developed. Lacking cement to round it off, the occlusal surface is very rough, even sharp-pointed in an unworn stage. Variations in shape of crown may be expressed by ratios between the anteroposterior diameter and the transverse diameter. These ratios vary in Dm_2 from 1.98 to 2.31; in Dm_3 , from 1.69 to 1.90; in Dm_4 , from 1.74 to 2.05.

The enamel pattern of the lower milk molars is simple. The maximum crown height is as follows: Dm_1 , 5 mm.; Dm_2 , 16 mm.; Dm_3 , 18 mm.; Dm_4 , 22 mm. The measurements were made on unworn milk teeth. The measuring points were taken on the posteroexternal face of the tooth from the base of the hypoconid to the crest of the hypoconid cusp.

Comparative measurements (in millimeters) of dentition of Merychippus calamarius

	C. I. T. no. 2839	C. I. T. no. 669	C. I. T. no. 1311	C. I. T. no. 2840	C. I. T. no. 2841	Type specimen Santa Fe
Upper dentition:						
Length of series P^2-M^3	135	133	142	134	129.0
Length of series P^2-P^4 . . .	76.6	73.5	71.3	74.7	71.7	67.8
Length of series M^1-M^3	61.4	61.9	67.2	61.9	61.0
P^1 , anteroposterior diameter	14.9	13.5
P^1 , transverse diameter . .	8.4	7.2
P^2 , anteroposterior diameter	29.3	27.5	27.0	27.0	27.4	25.0
P^2 , transverse diameter . .	16.9	17.5	17.4	18.2	17.9	17.8
P^3 , anteroposterior diameter	24.0	23.0	22.0	24.1	22.3	21.5
P^3 , transverse diameter . .	20.0	20.5	20.0	20.5	22.1	21.0
P^4 , anteroposterior diameter	23.3	23.0	22.3	23.6	22.0	21.0
P^4 , transverse diameter . .	21.0	21.9	21.1	21.5	22.8	20.5
M^1 , anteroposterior diameter	21.0	19.7	19.8	21.2	20.7	19.4
M^1 , transverse diameter . .	19.6	21.4	20.8	21.8	24.2	19.6
M^2 , anteroposterior diameter	22.5	21.2	19.8	23.0	21.2	21.2
M^2 , transverse diameter . .	20.5	21.6	21.3	21.8	24.2	18.9
M^3 , anteroposterior diameter	20.5	22.3	23.0	20.0	19.1
M^3 , transverse diameter	17.9	20.1	19.0	21.4	17a
I^1 , greatest diameter . . .	13.4	13.5	11.5			
I^1 , least diameter	8.1	8.0	8.0			
I^2 , greatest diameter . . .	13.8	14.5	13.6			
I^2 , least diameter	7.0	7.3	7.8			
I^3 , greatest diameter . . .	11.7	13.6	11.4			
I^3 , least diameter	5.8	6.3	6.4			
C, greatest diameter	10a	10.7	10.1			
C, least diameter	7.0	7.3			
Diastema, I^3-C	23.0	19.0	21.9			
Diastema, $C-P^1$	27.5	31.3			

a, approximate.

Continued on next page

Comparative measurements - Continued

	No. 2834	No. 2842	No. 678	No. 2837	Type
Lower dentition:					
Length of series P ₂ -M ₃	144	140	132*
Length of series P ₂ -P ₄	73.4	70.2	67
Length of series M ₁ -M ₃	70.6	69.4	65*
P ₁ , anteroposterior diameter	8.7
P ₁ , transverse diameter	5.0
P ₂ , anteroposterior diameter	24.6	24.4	22.9
P ₂ , transverse diameter	11.6	11.5	11.8
P ₃ , anteroposterior diameter	23.2	22.9	22.8	20.0
P ₃ , transverse diameter	13.6	12.8	14.5	13.2
P ₄ , anteroposterior diameter	24.3	23.1	20.3	21.4
P ₄ , transverse diameter	14.7	13.7	14.7	12.7
M ₁ , anteroposterior diameter	21.4	22.0	21.0	19.5
M ₁ , transverse diameter	12.8	11.5	12.0	10.5
M ₂ , anteroposterior diameter	21.3	23.3	20.0	18.6
M ₂ , transverse diameter	12.3	10.0	11.0
M ₃ , anteroposterior diameter	27.7	26.0	20.8*	24.8
M ₃ , transverse diameter	10.9	9.7	9.7	8.9
No. 2836					
I ₁ , greatest diameter	11.3	
I ₁ , least diameter	8.0	
I ₂ , greatest diameter	12.4	12.8	
I ₂ , least diameter	7.8	7.5	
I ₃ , greatest diameter	12.3	
I ₃ , least diameter	6.7	
C, greatest diameter	8.8	8.8	
C, least diameter	7.0	6.8	
Diastema, C-P ₂	42	49	

*Measurement does not include posterior lobe of M₃.

	No. 2843	No. 2844
Upper milk dentition:		
Length of series Dm ² -Dm ⁴	82.5	80.3
Dm ¹ , anteroposterior diameter	12.0
Dm ¹ , transverse diameter	7.0
Dm ² , anteroposterior diameter	34.0	30.5
Dm ² , transverse diameter	19.0	18.2
Dm ³ , anteroposterior diameter	23.7	22.9
Dm ³ , transverse diameter	21.7	21.4
Dm ⁴ , anteroposterior diameter	25.0	24.5
Dm ⁴ , transverse diameter	21.4	21.7
Di ¹ , greatest diameter	12.7
Di ¹ , least diameter	5.2
Di ² , greatest diameter	11.5
Di ² , least diameter	5.1
Di ³ , greatest diameter	9.7
Di ³ , least diameter	4.7
No. 656 No. 660		
Lower milk dentition:		
Length of series Dm ₂ -Dm ₄	82.4	77.3
Dm ₁ , anteroposterior diameter	3a
Dm ₁ , transverse diameter	4a
Dm ₂ , anteroposterior diameter	29.9	26.6
Dm ₂ , transverse diameter	13.8	12.4

a, approximate.

Comparative measurements - Continued

Lower milk dentition - continued:	No. 656	No. 660
Dm ₃ , anteroposterior diameter	24.6	24.0
Dm ₃ , transverse diameter	14.0	14.2
Dm ₄ , anteroposterior diameter	26.6	25.9
Dm ₄ , transverse diameter	13.3	13.5
D ₁₁ , greatest diameter	12.3	
D ₁₁ , least diameter	5.5	
D ₁₂ , greatest diameter	12.3	
D ₁₂ , least diameter	5.2	
D ₁₃ , greatest diameter	9.0	
D ₁₃ , least diameter	5.5	

Relationships. Unfortunately the neighboring Esmeralda localities (Stirton, 1936, p. 183) contain very scant protohippine remains. Of these only an M₃, U.C. no. 19825 (Merriam, 1916a, pp. 187-188, fig. 21), offers diagnostic characters which approach those of *Merychippus calamarius*. The occlusal surface of this tooth is short. The anteroposterior diameter of the metaconid-metastylid column and of the posterior lobe are relatively much shorter than the corresponding features in third molars from Tonopah. The relative transverse width of the posterior lobe of M₃ surpasses that in *M. calamarius*. The inflation of the entoconid and absence of an anteroexternal fold in this instance seem to signify little as to the evolutionary stage of the tooth. The crown height of 36 mm. may be considered extremely great for a merychippine tooth as worn as this one is. In summary, the strong development of the third lobe and the relatively great height of crown may be taken as evidence that this specimen, U.C. no. 19825, probably belongs to a primitive form of the genus *Protohippus* or *Plihippus*. Merriam (1916a, p. 188) stated that the tooth "represents a protohippine horse of approximately the stage of evolution seen in the form of *Merychippus* near *calamarius* of the Barstow fauna." To the author the tooth appears to be more advanced than *M. calamarius*, though its geologic age relative to the Tonopah merychippine horses cannot be stated with any surety.

Merychippus intermontanus Merriam (1915, 1919) from the Barstow fauna falls within the size limits of the largest individuals from Tonopah. A simple enamel pattern and early attachment of the protocone distinguish the upper cheek teeth and milk dentition from those of *M. calamarius*. None of the lower teeth of *M. intermontanus* carries the anteroexternal fold which develops so commonly in lower cheek teeth of *M. calamarius*.

Though the upper cheek teeth of *Merychippus sumani* Merriam (1911a, 1915, 1919) from the Barstow show a complexity of enamel pattern equal to that of *M. calamarius*, they are considerably smaller.

Merychippus calamarius stylodontus Merriam (1915, 1919) from the Barstow fauna closely approximates the Tonopah form in size, although the latter is larger. Furthermore, the enamel pattern of the Tonopah form is slightly more complex than that of the Barstow form. Merriam states (1919, p. 484) that *M. calamarius stylodontus* differs from the typical *M. calamarius* "in

relative simplicity of enamel folds of the walls bordering the fossettes. . . . It is considerably smaller than the typical form and the crowns seem narrower. The apparent difference in width may be due in part to differences in stages of wear of specimens compared, or to method of measurement." The author wishes to point out that the measurements previously recorded (Cope, 1877, p. 322; Merriam, 1919, p. 489) for *M. calamarius* obviously do not correspond to measurements made on the original plate (Cope, 1877, pl. 75, fig. 1). Thus discounting the question of width, it becomes apparent that *M. calamarius stylodontus* differs from the type *M. calamarius* in precisely the same manner as it does from the Tonopah merychippine species.

The teeth of the type *Merychippus calamarius* (Cope, 1875) from the Santa Fe do not differ from those of its equivalent from Tonopah in any important character. The upper teeth of the Santa Fe type may be described as slightly smaller and slightly more complex than typical Tonopah specimens. The lower teeth from Santa Fe show a relatively smaller posterior lobe in M_3 and they do not carry any anteroexternal fold.

Plication	Tonopah	Santa Fe
P11 caballin	Generally single	Single or double
P11 protoloph	Single, rare	Single, rare
P11 protoconule on P^2	Absent	Present
on other teeth	Single	Single
P11 prefossette on P^2	Single	Single
on other teeth	Generally single	Double to quadruple
P11 postfossette	Double or triple	Double or triple
P11 hypostyle	Absent or single	Single or double

The material from Quatal Canyon (Gazin, 1930) which was designated *Merychippus sumani* Merriam suggests but does not approach *M. calamarius*. The upper teeth from Quatal Canyon are smaller, less cemented, and lower-crowned than those of *M. calamarius*. The lower teeth in the Quatal Canyon collection differ from *M. calamarius* in having a more shallow inner gutter, a deeper, more rounded external valley, and a smaller posterior lobe on M_3 .

No teeth from the Mint Canyon fauna (Maxson, 1930; Stirton, 1933) approach those of *M. calamarius* in appearance.

The Ricardo species *Pliohippus tantalus* Merriam, U.C. no. 19434 (1913c, fig. 4; 1919, fig. 189), and *Pliohippus fairbanksi* Merriam, U.C. no. 19789 (1915, fig. 8; 1919, fig. 185), have both larger and higher-crowned teeth than does *Merychippus calamarius*. *Pliohippus* near *mirabilis* (Leidy), U.C. no. 21323 (Merriam, 1919, fig. 188), is of about the same size as *M. calamarius*, but its enamel pattern is simpler and the tooth crown appears to be higher.

None of the protohippine horses of the Great Plains region approaches very closely *M. calamarius* from Tonopah. The bulk of the Equidae from the Snake Creek was at first tentatively referred to *Merychippus* cf. *insignis* Leidy (Matthew and Cook, 1909). Later, when the formation was divided into zones,

90 to 95 per cent of the Equidae from the Lower Snake Creek were referred to *Merychippus paniensis* Cope (Matthew, 1924). The type for *M. insignis* consists of Dm^2 and Dm^3 . These teeth differ from *M. calamarius* in being noticeably smaller and in lacking cement. The type *M. paniensis* is smaller and relatively low-crowned, though Matthew does state that some of the specimens in the fauna are as large and progressive as *M. calamarius*.

Among the Niobrara River (*sensu* McGrew and Meade, 1938) protohippines in the undescribed collections of the University of California, *Merychippus insignis* appears much smaller and perhaps more primitive than *M. calamarius*. A second species represented by U.C. no. 33068 (perhaps *M. republicanus*) differs in its constant protoconal separation, smaller size, and slightly more complex enamel pattern. A third species, which may represent *M. perditus*, appears longer-crowned and shows definite connection between protocone and protoconule at a very early stage of wear.

Pliohippus supremus, U.C. no. 32285, from the Burge (McGrew, 1938) is somewhat similar to *M. calamarius* in size and in enamel pattern, but it is longer-crowned and the protocone becomes attached at a much earlier stage of wear. Teeth of *Pliohippus pernix*, U.C. no. 32501, are larger and simpler than those of *M. calamarius*, and display an attachment of the protocone at an earlier stage of wear.

Comparative Osteology of Hypohippus and Merychippus

Skeletal parts. For the sake of convenience in discussion, the skeletal elements of *Merychippus calamarius* and *Hypohippus* near *affinis* are described together. Very few of the larger bones have been preserved completely. The hypohippine material occurs in a poorer state of preservation and specimens are much less abundant than those of the merychippine type. The ratio of frequency of occurrence is 2 to 10 merychippine elements to every one of *Hypohippus*.

For the most part, the skeletal material resembles that of *Equus* very closely in all features except size. Only those differences from *Equus* which appear in form and in the proportions of elements are described below at some length.

Scapula. In this element of the shoulder girdle the spine differs from that of *Equus* in its downward slope toward the neck without suggestion of an acromion.

Measurements (in millimeters) of scapula

	<i>Merychippus</i> C.I.T. no. 759	<i>Hypohippus</i> C.I.T. no. 2888
Anteroposterior diameter from tuber to posterior border of glenoid cavity	68	77.5
Transverse diameter across glenoid cavity .	40	49
Anteroposterior diameter across glenoid cavity	44	56

Humerus. The head of the humerus is similar to that in *Equus*. In every other feature the humerus of *Merychippus* (fig. 5) differs from that of the modern horse. The bicipital groove is single, not double as in *Equus*. The anterior part of the lateral tuberosity is strongly produced so as to curve medially, and overhangs the bicipital groove. A large inner tuberosity extends posteriorly toward the articular surface of the head. The comparatively slender shaft is twisted. As compared with the corresponding feature in *Equus*, the deltoid ridge is inconspicuous and localized, having no crests extending out from it. The lateral condyloid crest is moderately developed. The coronoid fossa is not so deep as in *Equus*. The medial condyle is large and tapers from the medial border toward the synovial fossa. The lateral condyle is much smaller than the medial one, and medially is characterized by a low, rounded ridge. The lateral part of the lateral condyle is cylindrical rather than conical on its bearing surface. The forms of the medial and lateral condyles give the distal extremity a much more pronounced appearance of obliquity than is characteristic of *Equus*.

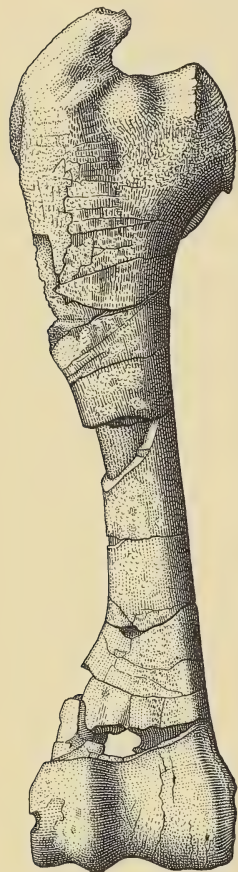


Fig. 5. *Merychippus calamarius* (Cope).

Right humerus, no. 2863,
anterior view. $\times 0.5$.

Calif. Inst. Tech.

Vert. Pale. Coll.

Upper Miocene, Tonopah,
Nevada

In all these characters in which the humerus of *Merychippus* differs from that of *Equus*, it shows a strong similarity to that of a Recent artiodactyl such as the ox.

In the later evolution of the horses from the merychippine stock there has developed in the humerus a double bicipital groove with a median convexity (Osborn, 1930, p. 754; Scott, 1895, p. 101). The curved and overhanging prominence of the anterior part of the lateral tuberosity has been subdued and finally lost. The deltoid ridge and its accompanying proximal and distal crests have become strongly developed.

Only the distal ends of several humeri of *Hypohippus* are available in the Tonopah collections. These differ from the merychippine type and approximate closely in form the humerus of *Equus*. The lateral condyloid crest is fairly well developed. The medial condyle does not taper so strongly as it does in *Merychippus*, yet it is not quite so gently tapering as in *Equus*. The lateral condyle is marked by a pronounced shallow groove and is conical, increasing in diameter toward the lateral border as in *Equus*. The distal extremity of the humerus differs from that of *Equus* in having a rounded border at the median side of the medial condyle, whereas in *Equus* the bearing surface of this condyle is separated from the median border by a very sharp angular break.

Measurements (in millimeters) of humerus

	<i>Merychippus</i> C.I.T. no. 2863	<i>Hypohippus</i> C.I.T. no. 2889
Total length	223	...
Smallest diameter of shaft:		
Anteroposterior	27	...
Transverse	22	...
Transverse diameter, proximal end	62	...
Transverse diameter, distal end	52	61

Radius. The humeral articular surface as well as the distal end of the radius of *Merychippus* differs from that of *Equus* in being proportionally narrower transversely. The sagittal ridge of the proximal end is a little more pronounced than it is in *Equus*. The dorsal surface of the shaft is strongly curved but the volar surface is flat.

Measurements (in millimeters) of radius

	<i>Merychippus</i> C.I.T. nos. 2864, 2865	<i>Hypohippus</i> C.I.T. no. 1308
Total length	227	265a
Proximal end, anteroposterior diameter	27.0	33.5
Proximal end, transverse diameter	50.0	59.0
Distal end, anteroposterior diameter	27.0	32.0
Distal end, transverse diameter	44.5	49.5

a, approximate.

Ulna. Only fragments of the proximal end of the ulna are preserved. The structural characters of the proximal end are similar to those in the corresponding parts of the ulna in *Equus*.

Carpus. The scaphoid does not differ markedly from that of *Equus*. In the merychippine form this element has rounder articular surfaces and more concave borders. The lunar resembles that of *Equus* very closely. The proximal articular surfaces of the cuneiform are relatively farther apart than in *Equus*. These surfaces are always distinct from each other, with a nonarticular area between them. The anterior proximal articular surface and the distal articular surface are relatively narrower than those of *Equus*. The pisiform is longer anteroposteriorly than in *Equus*. It has two distinct surfaces for articulation with the cuneiform and one surface which articulates with the ulnar part of the fore-leg bone. The trapezium was not preserved. The trapezoid is a wedge-shaped bone with less articulating surface than in *Equus*. It never has a posterior facet for articulation with the magnum. It may or may not bear a posterior facet for articulation with the trapezium. The magnum is much narrower transversely than the corresponding bone in *Equus*. The unciform resembles that of *Equus*. The posterior surface for articulation with the magnum, however, is smaller than in the modern horse. A small posterior articular surface for metacarpal V is usually present.

In summary, the carpal bones of *Merychippus* and *Hypohippus* differ but little from each other in shape and proportions. In the course of evolution

from *Merychippus* to *Equus* the carpals were shortened anteroposteriorly, widened transversely, and flattened proximodistally.

Measurements (in millimeters) of carpals

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

All measurements are minimum over-all diameters.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. nos. 2866-2872			C.I.T. nos. 2890-2896		
	AP	Tr	PD	AP	Tr	PD
Scaphoid	26.0	17.5	19.7	29.3	20.0	23.6
Lunar	24.1	19.4	19.0	27.0	19.7	23.0
Cuneiform	24.0	11.2	15.0	32.5	15.3	20.0
Pisiform	31.4	7.6	20.9	35e	8.0	22
Trapezoid	12.9	12.5	12.4	15.6	14.0	16.0
Magnum	23.9	25.2	16.5	30.3	30.0	19.7
Unciform	18.5	11.7	16.2	22.4	12.2	20.4

e, estimated.

Metacarpus. The proximal end of metacarpal III in both *Merychippus* and *Hypohippus* is not so broad as in *Equus*. For both Miocene types the angle between the magnum and unciform articular facets varies from 107° to 120° and averages 116° (cf. 160° in *Equus*). *Merychippine* metacarpal III is broadly grooved on its volar surface between the rough areas for attachment of the lateral metacarpals. The volar groove appears deeper in *Hypohippus*. In both *Merychippus* and *Hypohippus* the keel on the distal articular surface of metacarpal III is strong posteriorly, but weak to totally absent on the anterior surface. In *Equus* this keel is strong all the way around.

Lateral metacarpals II and IV are well developed in both *Merychippus* and *Hypohippus* (pl. 8). The hypohippine side metacarpals are readily distinguished from the more slender merychippine forms by their massiveness. In both genera metacarpal II bears a facet for articulation of the trapezium. On the posterior side of its proximal end, metacarpal IV carries a small facet for the articulation of metacarpal V. Below this small facet and parallel to the main axis of the metacarpus is a broad, flat, slightly roughened area against which lay metacarpal V.

Measurements (in millimeters) of metacarpus

AP, anteroposterior diameter.

Tr, transverse diameter.

These measurements were made on mounted specimens. The approximations are controlled by measurements of unmounted specimens of the same general size.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. no. 2854 (1)			C.I.T. no. 2856 (2)		
	II	III	IV	II	III	IV
Length	153	163	147	177a	192	173a
Proximal end, AP	12	19	14	13	22	15
Proximal end, Tr	9	26	10	12	28	13

a, approximate.

Measurements of metacarpus - Continued

	<i>Merychippus</i> C.I.T. no. 2854 (1)			<i>Hypohippus</i> C.I.T. no. 2856 (2)		
Distal end, AP	15	20	15	18	22	19
Distal end, Tr	8	25.5	7	11	27.5	11
Least dimensions of shaft:						
AP	7	14	8	12	15	12.5
Tr	6	18	4	6	22	6

(1) *Merychippine* metacarpal III varies in length between 160^o and 186 mm., and averages about 180 mm. long. Hence, this mounted specimen (C.I.T. no. 2854) is much smaller than the average for the Tonopah collection.

(2) *Hypohippine* metacarpal III varies in length from 183 to 192 mm., and averages 186 mm. The mounted specimen (C.I.T. no. 2856) is therefore larger than the average.

Pelvis. The acetabulum is the only part of the pelvic girdle which has been preserved. The *merychippine* acetabulum appears to resemble closely that of *Equus*. A single *hypohippine* acetabulum appears to be deeper and more nearly hemispherical than the others.

Measurements (in millimeters) of acetabulum

	<i>Merychippus</i> C.I.T. no. 2874	<i>Hypohippus</i> C.I.T. no. 2898
Anteroposterior diameter	42.0	46.5
Transverse diameter	33.0	46.8

Femur. No complete femora are preserved in the collection. The proximal and distal ends of the femur of *Merychippus* closely resemble those of *Equus*. The shaft of the femur is proportionately more slender than in *Equus*, but the lesser trochanter and the third trochanter are well developed.

A distal end of a *Hypohippus* femur shows a trochlea proportionately much narrower than in *Equus*. The lateral condyle of the femur in *Hypohippus* is much larger than the medial condyle, whereas in *Equus* the lateral condyle is only slightly larger.

Measurements (in millimeters) of femur

	<i>Merychippus</i> C.I.T. no. 2875	<i>Hypohippus</i> C.I.T. no. 2899
Length, estimated	275
Distal end, transverse diameter	61.5	76.5

Tibia. The tibia of *Merychippus* closely resembles that of *Equus* throughout. The shaft is slightly larger than that of *Equus* in proportion to the size of the extremities. The articular grooves of the distal end are slightly deeper and sharper in the tibia of *Merychippus*.

The distal end of a *hypohippine* tibia resembles that of *Equus* in every feature except a proportionately broader intermediate ridge on the articular surface.

Measurements (in millimeters) of tibia

	<i>Merychippus</i> C. I. T. no. 754	<i>Hypohippus</i> C. I. T. no. 2900
Length	283
Distal end, transverse diameter	45	57

Patella. Patellae of *Merychippus* and *Hypohippus* resemble that of *Equus*, except that the base is slightly more produced and the medial angle is less produced. These proportions give the bone the appearance of an elongate rhomb, when viewed from the front, rather than that of a square as in *Equus*.

Measurements (in millimeters) of patella

	<i>Merychippus</i> C. I. T. no. 2876	<i>Hypohippus</i> C. I. T. no. 2901
Anteroposterior diameter	25	28a
Transverse diameter	41	45a
Proximal-distal diameter	46	55a

a, approximate.

Tarsus. A deep, narrow groove bordered by narrow, high ridges characterizes the trochlea of a merychippine astragalus, in which respect the principal element of the tarsus resembles that in *Equus*. The hypohippine astragalus, in contrast, has a trochlea with broad, shallow groove bounded by low, wide ridges. The merychippine astragalus further resembles that of *Equus* in having on the navicular facet a well defined nonarticular depression, which is either poorly represented or entirely absent in the hypohippine astragalus.

In the merychippine calcaneum, and to a lesser extent in the hypohippine, there is a deeper groove between the tuber calcis (proximal part of the body) and the sustentaculum tali (medial process) than in *Equus*. The articular facet for the cuboid is slightly more steeply inclined upward and backward than the corresponding facet in *Equus*.

The astragalar facet of the navicular has a shallow nonarticular depression in the merychippine form and no depression in the hypohippine. Only 1 specimen in more than 60 naviculars of *Merychippus* has a surface for articulation with the calcaneum. This articulation occurs commonly in *Equus*. On the distal surface there is no nonarticular groove separating the two surfaces of articulation for the ectocuneiform. Likewise on the distal surface there is no nonarticular groove between the ecto- and mesocuneiform surfaces. Both of these grooves are commonly found in naviculars of *Equus*. Finally, in *Merychippus* the ento-mesocuneiform surface is continuous and rounded, not broken by an angle as in *Equus*. The fused ento-mesocuneiform bone in *Merychippus* and *Hypohippus* differs little from that in *Equus*.

In only 3 out of 42 merychippine ectocuneiform bones does the nonarticular groove completely cross the proximal surface. The distal nonarticular groove may vary in shape, but is never large as in *Equus*. Both these nonarticular grooves are far less developed in *Hypohippus* than in *Merychippus*. The proximal

posterior articulation for the cuboid appears to make a fairly constant angle with the proximal posterior articulation for the navicular in any given type of horse. Large series of measurements yield the following values: *Merychippus* 100° , *Hypohippus* 105° , and *Equus* 110° .

The cuboid of *Merychippus* differs from that of *Equus* in having the anterior surface for articulation with metatarsal IV relatively larger than the facet for metatarsal III. The posterior lateral surfaces for articulation with the navicular and ectocuneiform make a prominence which projects inward from the middle of the medial surface. In *Equus* this prominence lies near the posterior end of the medial surface. The cuboid of *Hypohippus* is shorter anteroposteriorly and more cuboid in shape than that of either *Merychippus* or *Equus*. Furthermore, all the articular surfaces on the hypohippine cuboid appear larger, especially the facet for metatarsal IV. In the cuboid bone of both *Merychippus* and *Hypohippus* the tuberosity for attachment of the plantar ligament is much larger than in *Equus*.

Measurements (in millimeters) of tarsals

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

All measurements are minimum over-all diameters.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C. I. T. nos. 2877-2882			C. I. T. nos. 2902-2907		
	AP	Tr	PD	AP	Tr	PD
Astragalus	28	36	42	32	42	44
Calcaneum	35	33	84	42	37	93
Navicular	26	30	10	31	31	12
Ento-mesocuneiform	11	25	14	15	29	18
Ectocuneiform	24	27	10	29	31	11
Cuboid	28	17	21	30	19	26

Metatarsus. In both *Merychippus* and *Hypohippus* the proximal end of metatarsal III presents a nearly circular anterior outline, in contrast with the oval outline in *Equus*. Whereas a facet for the articulation of the mesocuneiform is always present in metatarsal III of *Equus*, in *Merychippus* the facet appears in only 2 out of more than 70 specimens. On the other hand, this mesocuneiform facet seems to be present on all 7 well preserved hypohippine third metatarsals. In both *Merychippus* and *Hypohippus* the distal keel, though prominent on the posterior surface, dies away on the anterior surface. The transverse diameter of the distal end of metatarsal III is relatively much greater in *Hypohippus* than in *Merychippus*.

Lateral metatarsals II and IV are well developed in both *Merychippus* and *Hypohippus* (pl. 9). The merychippine side toes are much more slender than the hypohippine, especially near the distal end. The proximal end of metatarsal IV is very massive in both forms, and is characterized on the posterior side by a large sloping surface for the attachment of ligaments.

Measurements (in millimeters) of metatarsus

Ap, anteroposterior diameter.

Tr, transverse diameter.

These measurements were made on mounted specimens.

	<i>Merychippus</i>			<i>Hypohippus</i>		
	C.I.T. no. 2855 (1)			C.I.T. no. 2857 (2)		
Metatarsal	II	III	IV	II	III	IV
Length	170	183	171	202	217	203
Proximal end, AP	15	24	20	18	27	26
Proximal end, Tr	8	26	12	11	32	12
Distal end, AP	14	19	14	22	24	23
Distal end, Tr	8	25	7	12	33	14
Least dimensions of shaft:						
AP	6	16	5	13	18	15
Tr	2.5	18	3	5	24	5

(1) *Merychippine* metatarsal III varies in length between 182 and 216 mm., and averages 202 mm. Hence, this mounted specimen (C.I.T. no. 2855), almost the smallest in the collection, is much smaller than the average.

(2) *Hypohippine* metatarsal III varies in length between 212 and 221 mm., and averages 216 mm. This mounted specimen (C.I.T. no. 2857) is a little larger than average.

Phalanges. Owing to the variation in growth stages represented by the equids in the collection, the phalanges show considerable variability in size and proportions. Since no phalangeal series were found in undoubted association with upper limb bones, it is deemed undesirable to make distinction between the phalanges of the fore limb and those of the hind limb.

Digit III: The first phalanx of *Merychippus* is proportionally more slender than that of *Equus*, especially at the distal end. *Hypohippine* phalanx I, notably in the shaft, is much more robust than that of *Equus*. In the case of both *Tonopah* equids the median groove of the proximal articulation becomes shallower and disappears anteriorly. In *Equus* the groove is strong anteriorly as well as posteriorly. A single abnormal *merychippine* first phalanx in the collection, C.I.T. no. 2884, bears large lateral tuberosities or spurs which apparently functioned as aggrandized eminences for attachment of the collateral ligament. The form is in all likelihood a sport.

The *merychippine* second phalanx is longer and more slender than that of *Equus*. Proportionally, the second phalanx of the *Hypohippus* approximates that of *Equus* in length and breadth, but falls short in thickness of the distal end.

The third or ungual phalanx of *Merychippus* tends to be more slender and pointed than that of *Hypohippus*. Both are longer and narrower than the third phalanx of *Equus*. In the *Tonopah* forms the articular surface continues outward to the wings to make a bell-shaped pattern, as compared with the semicircular shape of the corresponding element in *Equus*. In the *Miocene* equids the wings, or angles, were either not developed or not ossified to the extent that they are in *Equus*. A well marked terminal cleft characterizes the ungual phalanges

of both *Merychippus* and *Hypohippus*. The angle of inclination between the ground plane and the anterior slope of the phalanx ranges from 33° to 35° in the Miocene forms, in contrast with approximately 50° in *Equus*.

The proximal sesamoids differ little except in size from those of *Equus*. No distal sesamoids were found in the entire collection.

Measurements (in millimeters) of digit III

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

These measurements were made on individual specimens in the collection and represent average-sized adults.

	<i>Merychippus</i> C.I.T. nos. 2885-2887			<i>Hypohippus</i> C.I.T. nos. 2908-2910		
	AP	Tr	PD	AP	Tr	PD
Phalanx I	42	43
Proximal end	22.5	30	...	25	36	...
Distal end	14	24	...	16	30	...
Least diameter of shaft	11.5	20	...	12.5	27.5	...
Phalanx II	30	34
Proximal end	19	30	...	21	35	...
Distal end	15	26	...	17.5	33	...
Least diameter of shaft	12.5	22.5	...	14	29	...
Phalanx III	37	37	24	41	40	25.5

Digits II and IV: The lateral phalanges are small and more variable in size than those of digit III. The hypohippine first phalanx is deeper proximally, much broader throughout, and slightly longer than that of *Merychippus*. The second phalanx of *Hypohippus* is longer and slightly larger than that of *Merychippus*. No lateral ungual phalanges are included in the collection.

Measurements (in millimeters) of digits II and IV

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

These measurements were made on individual specimens in the collection and represent average-sized adults.

	<i>Merychippus</i> C.I.T. nos. 2912-2913			<i>Hypohippus</i> C.I.T. no. 2911		
	AP	Tr	PD	AP	Tr	PD
Phalanx I	24.5	25.5
Proximal end	14.5	10.0	18.4	12.6
Distal end	11.0	9.3	11.5	11.5
Phalanx II	13.5	11.5	12.5			

RHINOCEROTIDAE

This family of the Perissodactyla is represented in the Tonopah fauna by relatively few specimens. The only well preserved material consists of first premolars followed by milk teeth in both upper and lower dentitions, along

with a few skeletal elements. Based upon the teeth, a population count of the rhinocerotids in the collection totals three individuals, one adult and two young. In the highly cristate pattern of its deciduous upper molars and in its retention of a large crested P^1 and a large simple P_1 , the Tonopah rhinocerotid appears distinct from any species previously described, and is designated as follows:

Aphelops? cristatus, n. sp.

(Plate 10; text figure 6)

Type specimen. A part of the left maxillary, C.I.T. no. 2806 (pl. 10, fig. 1), and a part of the left mandible, C.I.T. no. 2807. Specimen 2806 includes an unworn P^1 and slightly worn Dm^2 - Dm^4 . All the teeth are in good condition except for the middle part of the anterior end of Dm^2 , which has been lost. Specimen 2807 has the lower dentition which corresponds to that of the type maxillary, i.e., an unworn P_1 and slightly worn Dm_2 - Dm_4 . All are in good condition except Dm_2 . No. 2807 was found in the same horizon and only 2 feet from the maxillary. Undoubtedly it represents the lower jaw of the same individual.

Referred material. Dm^2 and Dm^3 , C.I.T. no. 762 (pl. 10, fig. 2); part of a ramus, C.I.T. no. 2808, bearing Dm_2 and Dm_3 ; a ramus, C.I.T. no. 2809, with Dm_2 - Dm_4 (pl. 10, fig. 3); tibia, fibula, calcaneum, two astragali, cuboid, three lateral metapodials, and a phalanx.

Specific characters. P^1 large, only slightly reduced, bearing an internal crest and three transverse cristae. Upper deciduous molars with several cristae always present, very strong crochet and moderate to strong antecrochet, union of crochet and crista occurring almost always. P_1 large, almond-shaped. Dm_2 long, very narrow, no protoconid-hypoconid valley. Limbs and feet normally proportioned as in modern rhinoceroses, not shortened as in *Teleoceras*.

Mandible. The young mandible, nos. 2807 and 2809, is quite slender and has very little depth. Much of this lack of depth may be ascribed to the youth of the individual, but the character reflects in part a customary shallowness of jaw in *Aphelops*. In mandible no. 2809, the depth of the inner side normal to the alveolar border, posterior to Dm_4 , is 53 mm.; height from lower border of angle to condyle, 146 mm.

Upper dentition. P^1 * is a small tooth with very simple crown consisting of an outer crest along the length of the tooth and a parallel inner crest which is restricted to the posterior part of the tooth. Three cristae run transverse to these crests. A large anterior crista and a small intermediate crista arise from the external crest, and the small posterior crista originates on the internal crest.

*Since the crown is not yet fully erupted and the following milk molars show considerable wear, the tooth is considered a P^1 . See Matthew, 1932, note on p. 423.

Dm^2 , a molariform tooth, is more elongate than the posterior deciduous teeth. The anterior border is diagonal and curved, giving the tooth an almost triangular outline. The outer wall is convex externally, and smooth except for a low style (parastyle fold) external to the paracone. The protoloph remains separate from the ectoloph until a very advanced stage of wear is reached. At this advanced stage a connection tends to be made by means of the median crest as well as by the anterior crest which projects inward from the ectoloph. There is no antecrochet arising from the protoloph; the prefossette is open. The relatively large metaloph is connected with the ectoloph. The metaloph bears a very strong crochet which joins the posterior crista from the ectoloph and closes off a median fossette. At least two small cristae from the ectoloph and one small crista from the crochet project into this median fossette. The postfossette is open. A low cingulum traverses the entire anterior, internal, and posterior border of the tooth. An internal tubercle, small to large in size, lies on the internal border of the tooth in the protocone-hypocone valley.

Dm^3 is wider transversely than Dm^2 and is larger and more nearly square in outline. The parastyle fold is much larger than in Dm^2 and relatively much farther forward because the parastyle is not so greatly produced anteriorly. The protoloph is firmly joined to the ectoloph and bears a bulky, rounded, but short antecrochet. The metaloph, slightly smaller than the protoloph, is firmly joined to the ectoloph by the posterior crista. A long relatively strong crochet folds forward from the metaloph. Union between the crochet and one of the two median cristae from the ectoloph is not consummated in one specimen, C.I.T. no. 2806, and only tenuously effected in another, C.I.T. no. 762. A few small cristae project into the region of the median fossette. None of the fossettes is really closed. A low cingulum and internal tubercle tend to develop as in Dm^2 . In no. 2806 a very small median ridge runs along the bottom of the protocone-hypocone valley.

Dm^4 in no. 2806 is almost identical in pattern and structure with Dm^3 of no. 762. In size, especially in crown height, Dm^4 bulks somewhat larger than Dm^3 .

Lower dentition. In ramus no. 2807, P_1 is just emerging. This tooth is almond-shaped. Instead of coming to a point, however, the occlusal surface is marked by an elongate fossette which opens into a groove on the internal side of the tooth. Two very small folds lie on the external wall of the tooth.

Dm_2 in no. 2808 is a long, very narrow, triangular tooth with lophoid pattern. It differs from permanent P_2 of other aphelopines in its length. The absence of any marked valley on the external wall differentiates the tooth from the second lower deciduous teeth in other aphelopines.

Dm_3 and Dm_4 , both relatively long-crowned, consist of two lophs arranged as in typical rhinocerotids. The only anomaly is a small internal cusp which lies in the posterior valley of Dm_4 .

Measurements (in millimeters) of dentition of Aphelops? cristatus

All measurements are minimum over-all diameters.

Upper dentition:	C.I.T. no. 2806	C.I.T. no. 762
Length of series P ¹ -Dm ⁴	154
Length of series Dm ² -Dm ⁴	138
P ¹ , anteroposterior diameter	27.0
P ¹ , transverse diameter	21.5
P ¹ , crown height	28a
Dm ² , anteroposterior diameter	46.0	50.0
Dm ² , transverse diameter	43.0	48.4
Dm ² , crown height	24.5	30.0
Dm ³ , anteroposterior diameter	48.0	53.6
Dm ³ , transverse diameter	47.0	52.0
Dm ³ , crown height	28.0	34.0
Dm ⁴ , anteroposterior diameter	54.0
Dm ⁴ , transverse diameter	52.5
Dm ⁴ , crown height	38.0

	No. 2807	No. 2809
Lower dentition:		
Length of series P ₁ -Dm ₄	155
Length of series Dm ₂ -Dm ₄	133	135
P ₁ , anteroposterior diameter	16e
P ₁ , transverse diameter	8e
P ₁ , crown height	22a
Dm ₂ , anteroposterior diameter	35a	38
Dm ₂ , transverse diameter	17.8	18.5
Dm ₂ , crown height	23.0	27.0
Dm ₃ , anteroposterior diameter	47.0	45.5
Dm ₃ , transverse diameter	22.0	22.0
Dm ₃ , crown height	29.0	32.0
Dm ₄ , anteroposterior diameter	46.0	49.0
Dm ₄ , transverse diameter	25.2	24.0
Dm ₄ , crown height	34.0	37.0e

a, approximate.

e, estimated.

Scapula. The massive scapula, C.I.T. no. 2811, bears no acromion. The tuber is large and rugose with a short, heavy coracoid process. Anteroposterior diameter from tuber to posterior border of glenoid cavity, 123 mm.; transverse diameter across glenoid cavity, 69 mm.; anteroposterior diameter across glenoid cavity, 88 mm.

Tibia and fibula. The thick-set tibia, C.I.T. no. 1310, differs little from the characteristic rhinocerotid form. Only the extremities of the fibula are preserved. The tibial facet of the distal extremity of the fibula makes a very obtuse angle (approximately 145°) with the astragalar facet, in contrast with a presumably more acute angle on the teleocerine form. Length, 400 mm.; transverse diameter of distal end, 101 mm.

Astragalus. The trochlear surface, which is long anteroposteriorly, has a characteristic deep and broad groove. The fibular facet is almost vertical. The external calcaneal facet presents a strongly concave and convex surface and is separated from the internal calcaneal facet by a deep nonarticular groove. The internal calcaneal facet is rounded in outline. The navicular

facet is relatively short anteroposteriorly. The cuboid facet makes a low angle with the navicular facet and is long, narrow, and diagonal in position. The posterior region of the line of junction between cuboid and navicular facets bears a distally projecting prominence.

Calcaneum. A short tuber calcis and a large astragalar facet which curves up onto the anterior side of the cochlear process characterize the calcaneum. The outline of the astragalar facet on the sustentaculum tali is rounded. The surface for articulation with the cuboid is strongly concave.

Measurements (in millimeters) of astragalus and calcaneum, C.I.T. no. 761

	AP, anteroposterior diameter.		
	Tr, transverse diameter.		
	PD, proximal-distal diameter.		
	AP	Tr	PD
Astragalus	54	90	78
Calcaneum	72	86	131

Cuboid. The most striking feature of the cuboid is the extremely large size of the tuberosity for the plantar ligament.

Metapodials. Three metapodials in the collection appear to represent metatarsal II (two specimens) and metatarsal IV (one specimen). These metatarsals are relatively long, slender, smooth, and strongly keeled distally (figs. 6a. 6b).

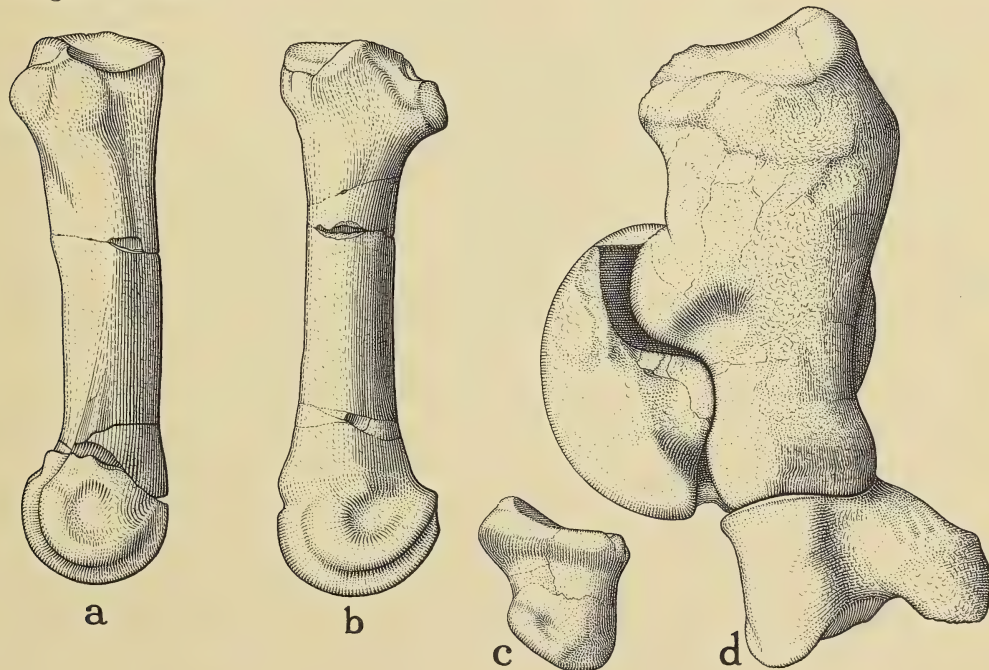


Fig. 6. *Aphelops? cristatus*, n.sp. Skeletal elements. a and b, metapodials, no. 2810; c, phalanx, no. 2812; d, calcaneum, astragalus, and cuboid, no. 761. Lateral views, $\times 0.5$.

Phalanx. A single side-toe phalanx I, though short, appears to be relatively narrow and high.

Measurements (in millimeters) of metatarsals and phalanx

AP, anteroposterior diameter.

Tr, transverse diameter.

	C.I.T. no. 2810 Metatarsals II IV		C.I.T. no. 2812 Digit II or IV, phalanx I
Length	142-162	141	37
Proximal end, AP	38	40	37
Proximal end, Tr	30	43	37
Distal end, AP	40	41	26
Distal end, Tr	31	31	29
Least dimension of shaft:			
AP	21	22	
Tr	23	26	

Relationships. The affinities of *Aphelops? cristalatus* clearly lie with *Aphelops* and *Peraceras* rather than with *Teleoceras*. In the absence of adequate skull material, however, the generic status of the Tonopah rhinoceros must remain tentative.

Aphelops malacorhinus Cope (Cope and Matthew, 1915, pl. 141) agrees closely with *A.? cristalatus* in respect to the broader points of size, tooth pattern, strong crochet, and weak antecrochet. It differs in having no cristae, and hence no union of crochet and crista to form a medifossette.

Aphelops mutilus Matthew (1924, 1932) is considered a progressive mutation of *A. malacorhinus*. It averages somewhat larger than *A.? cristalatus* in length of premolar tooth row and in transverse diameter of the teeth. The latter difference may be due in large part to the fact that the comparison is made between permanent teeth of one species and deciduous of the other. The teeth of *A.? cristalatus* are far more cristate than those of *A. mutilus*. This again may be a normal difference between milk and permanent teeth. P^1 of *A.? cristalatus*, however, is distinguished by a long external crest, a moderately long inner crest, and three transverse cristae. P^1 of *A. mutilus* and all other comparable rhinocerotids bear two internal cusps, of which the larger is posterior, rather than a single long crest. Transverse cristae are single or absent.

In view of these similarities and differences, *Aphelops? cristalatus*, progressive in tooth pattern but primitive in retaining well developed P^1_4 , is regarded as an offshoot of the line which gave rise to *A. malacorhinus* from the Republican River bed (exact fauna not known; Stirton, 1936, p. 188) and to *A. mutilus* from the Coffee Ranch Quarry and from Higgins Quarry A of Texas.

Aphelops ceratorhinus Douglass (1903) differs from *A.? cristalatus* in smaller size and in absence of antecrochets and cristae.

Aphelops megalodus (Cope, 1873; Cope and Matthew, 1915) from Pawnee Creek is much smaller and distinctly more primitive in all its tooth characters.

Aphelops meridianus (Leidy) and material from New Mexico assigned to the species by Cope (1877, pp. 317-319, pls. 73, 74) is likewise a small and primitive form.

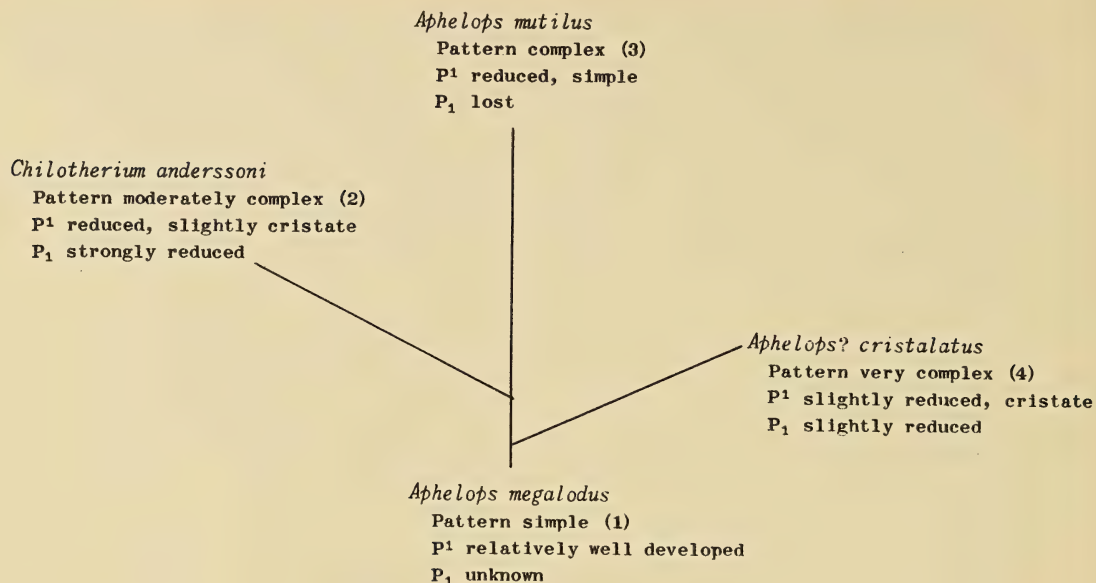
Until *Aphelops jemezianus* Cope (1877, pl. 73) is represented by better and more abundant material it will be impossible to determine any but its broadest relationships. No satisfactory comparison can be made between *A. jemezianus* and *A.? cristalatus*.

An upper milk molar from the valley of the Niobrara River was described and illustrated by Leidy (1858, p. 28; 1869, pl. 23, figs. 4, 5). The tooth resembles Dm^3 (C.I.T. no. 2806) of *A.? cristalatus* very closely in pattern. The Niobrara River tooth is of indeterminate genus and species (Matthew, 1918, p. 207, without any specific reasons refers the tooth to *Teleoceras fossiger*).

Aphelops sp. Matthew (1918, fig. 13, A.M.N.H. 17222), consisting of P^1 - Dm^4 , represents a form which is much smaller, with simpler tooth pattern, than that from Tonopah. The inner crest of so-called Dm^1 (probably P^1) consists of two rudimentary cusps rather than an elongate crest. No cristae are present, hence in no tooth of the series does the crochet unite with a crista to form a medifossette. A not far distant ancestor of *Aphelops? cristalatus* may have resembled this (Lower?) Snake Creek *Aphelops* sp. very closely.

As Matthew has conclusively demonstrated (Matthew, 1932, pp. 433-435), "Among the Old World Rhinocerotidae the group of species assembled by Ringström under *Chilotherium* make the nearest approach to the American *Aphelops*." An illustration of the milk dentition of *Chilotherium anderssoni* Ringström (1924, pl. 3) emphasizes the similarity between this Asiatic rhinocerotid of the *Hipparion* fauna and the American *Aphelops? cristalatus*. The milk teeth of *Chilotherium anderssoni* are of same length as those of the Tonopah form, but they are narrower transversely and are progressively higher-crowned from P^1 through Dm^2 to Dm^4 . The outer crest and three transverse cristae of P^1 resemble *A.? cristalatus* in form, but the metaloph is a conical cusp as in all species of *Aphelops* except *A.? cristalatus*. In each of the milk molars, Dm^2 to Dm^4 , the main medial crista is well developed, but there are no minor cristae such as appear in *A.? cristalatus*. The antecrochet and the posterior part of the cingulum are more strongly developed in *Chilotherium* than in *Aphelops*. In the lower jaw, P_1 is a peglike tooth which is absent in most cases, in contrast with the relatively well-developed P_1 of *A.? cristalatus*. Dm_2 to Dm_4 are almost identical with the corresponding teeth of the Tonopah species, except that there is a strong protoconid-hypoconid valley in Dm_2 , a feature which is characteristically absent in *A.? cristalatus*.

On the basis of dentition alone the following relationships seem indicated:



(1) Simple: No crista; no crochet; weak antecrochet.

(2) Moderately complex: Crista present or absent; strong crochet; moderate to strong antecrochet; occasional union of crochet and crista on premolars.

(3) Complex: Crista always present; strong crochet; moderate to strong antecrochet; union of crochet and crista on premolars almost always.

(4) Very complex: Several cristae always present; very strong crochet; moderate to strong antecrochet; union of crochet and crista on premolars almost always.

An astragalus, U.C. no. 19824, from the Esmeralda can be assigned questionably to *Aphelops*.

Some fragmentary teeth from High Rock Canyon, U.C. no. 11619, suggest that their crown pattern was cristate when unworn. This material, though slightly larger, is comparable in size with C.I.T. no. 2807. Since the High Rock Canyon material represents adults, however, a direct comparison with the youthful *A.? cristatus* is almost meaningless.

CAMELIDAE

The family is sparingly represented in the Tonopah fauna. A fairly well preserved palate and a single partial ramus with P₂-M₃ provide the only moderately complete dentitions in the collection. The remainder of the collection consists of maxillary and mandibular fragments, isolated teeth, an axis, a few complete limb bones, many carpals, tarsals, and phalanges, a few metatarsals but no complete metacarpals, and an abundance of more fragmentary skeletal material.

An estimate based on the occurrence of astragali and teeth indicates that the fauna contained as a minimum population at least eight camelids, two young and six adults.

Alticamelus? stocki, n. sp.

(Plate 11; text figure 7)

Type specimen. A palate with P^1 - M^3 of both sides complete (except both P^2 's broken off), left C, right I^3 , both I^2 's, and the alveoli for both I^1 's, C.I.T. no. 1434 (pl. 11, figs. 1, 1a).

Paratype specimen. A ramus with P_2 - M_3 complete, C.I.T. no. 2819 (pl. 11, figs. 2, 2a).

Referred material. A palate, C.I.T. no. 764; symphyseal section of jaw, no. 2820; milk teeth Dm^3 and Dm^4 , no. 2821; Dm_3 and Dm_4 , no. 2822; axis, no. 2828; ulnoradii, nos. 2823 and 2824; tibia, no. 2825; metatarsi, nos. 2826 and 2827; and all (except perhaps the very largest) camelid carpals, tarsals, and phalanges in the Tonopah collection.

Specific characters. I^1 and I^2 retained in fully adult individual. Premolars slightly more reduced than in other species of *Alticamelus*. Limb bones large and long, but proportionally not quite so long as in other alticamelids. I take pleasure in naming this species for Dr. Chester Stock.

Skull. In the best-preserved palate, C.I.T. no. 1434, the posterior palatine foramen lies just medial to the middle of P^3 . This part is more anterior than the foramen in the second palate, no. 764. The relative shortness of all the diastemata constitutes an important diagnostic character.

Measurements (in millimeters) of diastemata

	C.I.T. no. 1434	C.I.T. no. 764
I^3 -C	11.5	16.0
C- P^1	15.0
P^1 - P^2	12.0	19.0

Mandible. The mandibular material is too fragmentary to display any important characters. A large mental foramen lies below P_1 , and a second and smaller foramen is situated between P_4 and M_1 . Depth of mandible no. 2819 below M_1 , 41 mm.; width of mandible below M_1 , 23 mm.; diastema I^3 -C, 15 mm.; diastema C- P_1 , 19 mm.; diastema P_1 - P_2 , est. 18 mm.

Upper dentition. There is a deep conical alveolus for a moderately large I^1 which projects anterolaterally. I^2 is somewhat smaller than the first incisor and the crown is perhaps nonfunctional. The tooth curves inward. I^3 is large, strong, and caniniform. The recurved canine bulks approximately as large as I^3 . Caniniform P^1 is a little more recurved than the canine and has a shorter crown, but its single root is just as massive as that of the canine.

The long, narrow, and double-rooted P^2 is relatively large and bears cingulum-like ridges on the internal wall at either end of the tooth. P^3 is similar to P^2 , but the internal ridge is developed along the whole internal wall of the tooth so that it closes off a long, narrow fossette. In P^4 the

internal wall reaches full development, being thick and strongly convex lingually. The premolars do not appear to be greatly reduced.

The molar teeth are large, simple, and typically camelid with their moderately high crowns (26 mm. on external side of an unworn tooth, C.I.T. no. 2831, measured from root to highest point in intercusp valley), very strong styles, and strong fold on the external enamel wall.

Lower dentition. The three strongly procumbent lower incisors are spatulate when unworn. The large canine and single-rooted P_1 , both caniniform, approximate each other in size.

P_2 is slender, simple, moderately large, and double-rooted. P_3 and P_4 are relatively little reduced. The molars are large, simple, and moderately high-crowned.

Milk dentition. Dm^3 is submolariform, with a strong anterior style, a narrow anterior crescent, and a posterior crescent. Dm^4 is slightly higher-crowned than Dm^3 . It is completely molariform, although smaller and lower-crowned than the true molars.

Dm_3 is a long and very slender tooth characterized by two deep infolds in its internal wall, one in its external wall, and a small enclosed posterior fossette. Dm_4 with its three crescents is long, slender, and only moderately high-crowned.

Measurements (in millimeters) of dentition of Alticamelus? stocki

All measurements are made approximately at the wearing surface of the teeth. In measuring anteroposterior diameters of molars and milk molars, the parastyle was not included. No. 1434 (upper dentition) represents a fully adult camelid, in which the anterior crescentic infold of M^1 has already partially disappeared with wear. No. 2819 (lower dentition) is so worn that the anterior crescent infold has disappeared in M_1 and is almost completely worn away in M_2 . The milk dentitions, both upper and lower, are little worn.

Upper dentition:	C.I.T. no. 1434
Length of series P^2-M^3	149
Length of series P^2-P^4	53
Length of series M^1-M^3	96
I^3 , anteroposterior diameter	11a
C , anteroposterior diameter	11.5
C , transverse diameter	9.5
P^1 , anteroposterior diameter	12.4
P^1 , transverse diameter	8.2
P^2 , anteroposterior diameter	14a
P^2 , transverse diameter	7.5a
P^3 , anteroposterior diameter	19.0
P^3 , transverse diameter	11.4
P^4 , anteroposterior diameter	18.0
P^4 , transverse diameter	17.5
M^1 , anteroposterior diameter	27.0
M^1 , transverse diameter	22.0
M^2 , anteroposterior diameter	35.5
M^2 , transverse diameter	24.0
M^3 , anteroposterior diameter	36.8
M^3 , transverse diameter	21.0

a, approximate.

Measurements - Continued

Lower dentition:		No. 2819
Length of series P ₂ -M ₃		144
Length of series P ₂ -P ₄		44
Length of series M ₁ -M ₃		100
P ₂ , anteroposterior diameter		11.4
P ₂ , transverse diameter		5.3
P ₃ , anteroposterior diameter		15.6
P ₃ , transverse diameter		6.4
P ₄ , anteroposterior diameter		17.7
P ₄ , transverse diameter		9.2
M ₁ , anteroposterior diameter		24.5
M ₁ , transverse diameter		15.5
M ₂ , anteroposterior diameter		32.3
M ₂ , transverse diameter		19.1
M ₃ , anteroposterior diameter		42.5
M ₃ , transverse diameter		16.1

Upper milk dentition:		No. 2821
Dm ³ , anteroposterior diameter		25.0
Dm ³ , transverse diameter		13.0
Dm ⁴ , anteroposterior diameter		24.0
Dm ⁴ , transverse diameter		14.0

Lower milk dentition:		No. 2822
Dm ₃ , anteroposterior diameter		17.0
Dm ₃ , transverse diameter		7.3
Dm ₄ , anteroposterior diameter		33.0
Dm ₄ , transverse diameter		10.5

Skeletal parts. In relation to the size of the dentition, the skeletal parts in the camelid collection appear inordinately large. Yet since but one type of camelid is found in the fauna, these dentitions and skeletal parts are presumed to be of the same species.

Axis. The second cervical vertebra (no. 2828, fig. 7e), though large, is not particularly elongated for a camel of this size. The odontoid process is spoutlike. Length of centrum, 200 mm.; transverse diameter at anterior end, 79 mm.

Ulnoradius. The radius and ulna are as firmly fused together as in Recent *Lama*. Two examples of this bone are preserved in the collection, one moderately large, presumably of a young animal, the other of a very large adult (figs. 7a, 7b).

Measurements (in millimeters) of radius

	C.I.T. no. 2823	C.I.T. no. 2824
Total length	448	575
Proximal end, transverse diameter	67	74
Distal end, anteroposterior diameter	47	55
Distal end, transverse diameter	65	77



Fig. 7. *Alticamelus? stocki*, n. sp. *a*, ulnoradius, no. 2724, anterior view; *b*, ulnoradius, no. 2823, anterior view; *c*, tibia, no. 2825, anterior view; *d*, metatarsus, no. 2826, anterior view; *e*, axis, no. 2828, lateral view; *f*, phalanx, no. 2858, anterior view; *g*, phalanx, no. 2859, anterior view. All figures $\times 0.33$.

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada

Carpus. The carpal elements differ little from those of Recent *Lama*, except in their somewhat larger size. Although the size of the carpals varies somewhat, there do not appear to be any distinctive characters by which the elements can be segregated.

Measurements (in millimeters) of carpals, C.I.T. nos. 2914-2920

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

All measurements are minimum over-all diameters. The series which was measured is of average size.

	AP	Tr	PD
Scaphoid	39	22	30
Lunar	38	24	34
Cuneiform . . .	40	24	33
Pisiform	49	24	38
Trapezoid . . .	22	16	21
Magnum	33	24	19
Unciform	46	26	28

Metacarpus. No complete metacarpal elements occur in the collection. The proximal end of a large cannon bone corresponds in size to the large carpals and the large ulnoradius. This large metacarpus is strongly fused as in an adult. A pair of smaller metacarpals, agreeing in size with the smaller radius and carpals, is not completely fused into one bone and hence may represent a young individual. The step down from the proximal articular surface of metacarpal-III to the articular surface of metacarpal IV is pronounced. Proximal end of metacarpus no. 2829, anteroposterior diameter, 45 mm.; transverse diameter, 59 mm.

Tibia. The long, fairly slender tibia of a young individual shows no noteworthy features (no. 2825, fig. 7c). The lateral malleolus is similar to that of *Lama*. Total length, 495 mm.; distal end, transverse diameter, 66 mm.

Patella. The patella, no. 2921, resembles that of *Lama*. Anteroposterior diameter, 30 mm.; transverse diameter, 38 mm.; proximal-distal diameter, 80 mm.

Tarsus. The tarsal bones of a young individual appear to correspond very closely to those of *Lama*. The astragalus is relatively narrow.

Measurements (in millimeters) of tarsals C.I.T. nos. 2922-2926

AP, anteroposterior diameter.

Tr, transverse diameter.

PD, proximal-distal diameter.

	AP	Tr	PD
Astragalus	37	40	64
Calcaneum	48	42	130
Navicular	39	25	23
Cuboid	50	31	27
Ectocuneiform . .	28	26	18

Metatarsus. The metatarsal bones of a young individual demonstrate that at first fusion is incomplete near the distal end of the shafts. Fusion is completed in an older, slightly larger individual. A few very large distal extremities of metapodials constitute some of the material which may represent a larger and different species of camelid. In Recent *Lama* the distal ends of the metacarpals are larger than the distal extremities of the metatarsals. Hence these large fragments need not necessarily represent another species, but may belong to the fore feet of an especially large individual. In C.I.T. no. 2827, the total length of the metatarsus is 407 mm.; transverse diameter of proximal end, 51 mm. The transverse diameter of the distal end of this specimen, a normal metatarsal, is 28 mm.; the corresponding measurement in no. 2830, a very large metapodial, is 36 mm.

Phalanges. In Recent *Lama* the phalanges of the manus may measure as much as one-ninth (11 per cent) larger in every dimension than do the phalanges of the pes. It is to be noted, however, that they maintain similar proportions in both manus and pes. Hence, in a collection of fossil camelid phalanges of a given species there should be little variation in proportions even though the size range seems considerable. On this account a few disproportionately massive phalanges may be associated with the metapodial material to represent a larger camelid.

Measurements (in millimeters) of phalanges

	AP, anteroposterior diameter.		
	Tr, transverse diameter.		
	PD, proximal-distal diameter.		
	AP	Tr	PD
Phalanx I, no. 2858 (normal specimen)	96
Proximal end	28	29	..
Phalanx I, no. 2859 (large specimen)	99
Proximal end	34	39	..

Relationships. At present the distinctions between the various Upper Miocene--Lower Pliocene camelids appear to be very poorly defined. Matthew (1901) reviewed the bases upon which these distinctions are made. When the structural features of the Tonopah camelid are compared with Matthew's revised list of generic characters (1918), the Nevadan type is found to differ from *Pliauchenia* and *Megatylopus* in having a complete dentition. The latter two genera have each but one incisor, and the premolar formulas are $\frac{3}{2}$ and $\frac{2}{2}$ respectively. *Miolabis* is much smaller and more primitive.

The Tonopah form differs from *Procamelus* in its complete dentition with not quite so much reduction of the premolars. The limb bones of the Tonopah camelid are relatively longer and larger.

Protolabis resembles *Alticamelus? stocki* only in the retention of its upper

incisors. It differs decidedly in its small, short limb bones and in the separate to imperfectly united metacarpals.

According to Stirton (1929, p. 293) there are a number of characters by which *Alticamelus* may be distinguished from *Procamelus*. The Tonopah material shows the following features diagnostic of *Alticamelus*: (1) The premolars are slightly less reduced than in *Procamelus*. (2) The parastyle, mesostyle, and anterior external rib are more prominent. (3) The diastemata between P^1 and P^2 and between C and P^1 are relatively short. (4) The P_1 - P_2 diastema (estimated) is much less. (5) The caniniform teeth are heavier than in *Procamelus*. (The upper canines in C.I.T. no. 1434 are of about the size seen in *Procamelus*, but I^3 and P^1 are larger. All the caniniform teeth are very large in no. 764.) (6) The first premolars, upper and lower, show no tendency to develop double roots. (7) The inner side of the lobes of the lower molars is slightly convex anteroposteriorly, but not much more so than in *Procamelus*.

All the characters listed above appear to be valid. Since the Tonopah camelid lies in or near the alticamelid group with respect to each of these characters, it apparently should be referred to the genus *Alticamelus*. If, however, the absence of the first and second upper incisors be considered a definite character of *Alticamelus*, then C.I.T. no. 1434, as a fully adult specimen with complete dentition, cannot be of that genus. In his description of *Alticamelus giraffinus*, Matthew (1901, p. 430, *A. altus*; Matthew and Cook, 1909, p. 402, renamed *A. giraffinus*) states that "the first and second upper incisors are represented by small crownless stumps, perhaps the remains of the milk dentition." The first two incisors in no. 1434 are much reduced in size and may have had little function, but their reduction is not so great as that described by Matthew and they are probably not milk teeth. Matthew (1924, fig. 54) has referred a figured specimen, A.M.N.H. nos. 18350 and 18869, to *Alticamelus* cf. *leptocolon*. The specimen is undescribed. The figure shows alveoli for all three incisors, but the specimen might be of the genus *Protolabis*.

Ratios of premolar reduction have been calculated by dividing the length of series M^1 - M^3 by that of P^2 - P^4 , and also by dividing the length of series M_1 - M_3 by that of P_2 - P_4 . These reveal that in all but one species of *Alticamelus* the premolar teeth are relatively less reduced than in nos. 1434 and 2819 from Tonopah. The one exception is an *Alticamelus* referred to *leptocolon*, A.M.N.H. nos. 18350 and 18869, by Matthew (1918). This ratio does not distinguish *Alticamelus? stocki* from *Protolabis* and *Procamelus*.

A second ratio was calculated to determine the limb proportions of the various Upper Miocene camelids. This ratio was derived by dividing the length of the series M_1 - M_3 into the length of the metacarpal. Where these measurements were not available, length M^1 - M^3 and length of metatarsal were used. It must be remembered that although the use of both of these "substitute" measurements gives approximately the same ratio, the use of only one

"substitute" may affect the ratio as much as several tenths of a point. Shortening of the tooth row with wear is another important source of error. This ratio actually does set apart the alticamelid group from the genera *Protolabis* and *Procamelus*. *Protolabis* has a much lower ratio. That of *Procamelus* is still lower. *Procamelus* with its moderately long limbs should have a higher ratio than available measurements indicate. Although additional material will probably yield higher ratios for *Procamelus*, these new ratios will undoubtedly remain distinctly lower than those for *Alticamelus*. In limb proportions *Alticamelus? stocki* falls nearest to the *Alticamelus* group, although it cannot be definitely included within that group.

Comparative measurements (in millimeters) and ratios of limb elements and tooth rows of Alticamelus

1. *A.? stocki*, Tonopah, C.I.T. For specimen numbers, see p. 153.
2. *A. alexandrae*, Barstow, U.C. no. 26015.
3. *A. procerus*, Lower? Snake Creek, A.M.N.H. no. 14070.
4. *A. sp. 1*, Snake Creek, undescribed (Davidson, 1923).
5. *A. giraffinus*, Pawnee Creek, A.M.N.H. no. 9109.
6. *A. leptocolon*, Pawnee Creek, A.M.N.H. no. 18350.

Lengths:	1	2	3	4	5	6
P ² -M ³	149	117.5	157	111
P ² -P ⁴	53	46.5	63	34
M ¹ -M ³	96	74.5	98	87	74
P ₂ -M ₃	144	130	164	143	154
P ₂ -P ₄	44	45.5	56	48	49
M ₁ -M ₃	100	84.5	108	95	105
Axis	200	172	250
Radius	448-575	480	494	417-464
Metacarpus	390	399*	362-389
Metatarsus	403	552	624.4	355
Ratios:						
Upper, m/pm**	1.81	1.60	1.55	2.18
Lower, m/pm	2.18	1.85	1.93	1.98	2.14
Metapodial	4.2	4.6	5.6	4.2	7.1	4.8
Molar tooth row						

*A metacarpus recorded for *Alticamelus sp. 1* (Davidson, 1923, p. 406) with length of 484 mm. is evidently not to be associated with a radius with length of 494 mm. Hence the metacarpus described as of *A. sp. 2* by Davidson and having a length of 399 mm. is used instead.

**Ratio between lengths of molar and premolar tooth rows.

Alticamelus alexandrae Davidson (1923) from the Barstow Miocene has no I¹ and I². The tooth row is shorter, the premolars are less reduced, and the limb bones are more elongate than in *A.? stocki*. The length of the axis is proportionally the same in both forms.

Alticamelus procerus Matthew and Cook (1909) from the Lower? Snake Creek differs from *A.? stocki* in absence of I¹ and I², in longer tooth row, in less reduced premolars, and in more elongate limbs.

Alticamelus giraffinus Matthew (1901, *A. altus*) from Pawnee Creek, an old individual with a longer tooth row and less reduced premolars, differs striking-

ly from the Tonopah species in the extreme elongation of its limb elements and of its neck. This species, the type of the genus, has the stumps of I^1 and I^2 .

The skull, mentioned above, which was referred by Matthew (1924, fig. 54) to *A. cf. leptocolon* has a much shorter tooth row than no. 1434, but I^1 and I^2 are present. Because of lack of further illustrations and detailed description of this camelid, the two forms cannot be closely compared. Limb bones which have been designated *A. leptocolon* Matthew (1901, fig. 30; 1909, p. 115) are of the same proportions as the specimens from Tonopah, but somewhat smaller.

Some undescribed alticamelid species from Snake Creek (Davidson, 1923, pp. 402, 406) approximate in measurements the Tonopah material. The premolars of the Snake Creek form are somewhat less reduced. *Alticamelus priscus* Matthew (1924, p. 187) lacks sufficient description for any detailed comparison.

ANTILOCAPRIDAE

A large number of merycodont remains, including skull parts and horn cores, have been described from the Tonopah locality (Furlong, 1934). On the basis of this material, two new species were established: (1) *Merycodus loxocerus* Furlong, represented by no less than sixty individuals of all ages, and (2) *Merycodus hookwayi* Furlong, known by the remains of possibly more than three individuals.

Considerable variation in size and pattern of merycodont horn cores can be noted in a collection of this kind of material from a given locality. Sometimes several distinct types are represented. More commonly the types grade by small variations from one to another. With such variations possible, it would seem logical to use minor structural differences in horn-core development to distinguish species or varieties. It is deemed advisable to reserve for generic distinction the differences in dental characters and the major differences in the horn cores.

Furlong has already pointed out the characters of horn core and dentition which serve to distinguish the two Tonopah species from all others. No attempt was made, however, to determine the phylogenetic position of these species.

The best criteria for establishing the relationships of merycodonts are not found in the form and size of the horn cores, but in the length of the postsymphyseal diastema, the reduction of the premolars, the crown pattern of P_4 , and the lengthening of the molar tooth crowns.

Frick has indicated the relative length of the postsymphyseal diastema by recording the ratio of the anteroposterior diameter of M_3 to the diastema length. The selection of the length of M_3 as dividend in the ratio, though moderately satisfactory for determining specific differences, is peculiarly unfortunate from the point of view of demonstrating the relative diastema length in species. The evolutionary trend in merycodonts is shown by an increase in size of M_3 as well as by an increase in length of diastema. Hence, with both

values increasing in the normal evolution of the family, the ratio between M_3 and diastema length may remain constant, even though both are greatly elongated relatively to the rest of the tooth row. Therefore, to emphasize more correctly the relative increase in diastema length, the anteroposterior diameter of M_1 is suggested rather than the corresponding measurement of M_3 .

The ratio of length of premolar tooth row to length of molar tooth row has been used to indicate the amount of shortening in the premolar series.

The phylogenetic significance of the crown pattern of P_4 was discussed in a previous paper (Henshaw, 1938, pp. 65-67).

The length of the molar tooth crowns is probably the most important character in determining phylogenetic relationships. Though well shown in Frick's illustrations (Frick, 1937, figs. 41-47), this character unfortunately has not been considered in any large measure by other students of the merycodont antelope group.

Merycodus loxocerus Furlong

Relationships. Measurements taken on C.I.T. nos. 713 and 1298 indicate that the postsymphyseal diastema is relatively extremely short, only those of *Ramoceros coronatus* (Merriam) (Frick, 1937, p. 437) and *Merycodus sabulonis* (Matthew and Cook, 1909, p. 411) being shorter. The premolar-molar tooth-row ratio in *M. loxocerus* indicates less reduction of the premolar tooth row than in any other merycodont except the primitive *Merycodus agilis* Douglass from Madison Valley. The crown pattern of P_4 often retains the primitive five-lobed form. The molar crown height on unworn teeth is very low in relation to anteroposterior length of tooth, e.g. in M_3 approximately 12 mm. crown height to 12 mm. anteroposterior length.

All these characters emphasize the primitive nature of *Merycodus loxocerus*. The type of horn core found in this species agrees closely with some of those from the Barstow, e.g. *Merycodus alticornis* (Frick, 1937, p. 347 and fig. 38A), described as "shaft unusually slender and elongate." The lower teeth of the Tonopah form, however, appear more primitive than those of the Barstow (Frick, 1937, figs. 46, 47).

Merycodus hookwayi Furlong

Relationships. Measurements taken on the paratype, C.I.T. no. 712, show that the postsymphyseal diastema of *Merycodus hookwayi* is relatively shorter than in all species except *Ramoceros coronatus*, *Merycodus sabulonis*, *M. loxocerus*, and *M. agilis*. The slight premolar shortening exceeds only that in the primitive forms *M. agilis* and *M. loxocerus*, and equals that in *Ramoceros coronatus* and *Merycodus sabulonis*. The crown pattern of P_4 , as in *M. loxocerus*, is of the five-lobed type. The height of crown of M_3 is 16 mm. on an unworn tooth 14.5 mm. long.

Merycodus hookwayi represents a primitive merycodont which is slightly more

advanced than *Merycodus loxocerus*. Frick placed *M. hookwayi* in the genus *Meryceros*, yet he characterized that genus as having muzzle and diastema elongate. Furthermore, the horn cores of typical *Meryceros* all appear to be short-shafted. *Merycodus hookwayi*, with its long though moderately heavy-shafted horn core, and above all its shortened diastema and heavy premolars, appears to be more closely related to Frick's subgenus *Paracosoryx*.

For reasons previously discussed (Henshaw, 1939, pp. 25-26), this Tonopah species is referred to the genus *Merycodus*. The subgenus *Paracosoryx* appears to be valid.

Among Frick's figured specimens the one which appears closest to *M. hookwayi* is F.A.M. no. 31159 (Frick, 1937, fig. 39A; also p. 347). Frick referred this Barstow specimen to *M. (Paracosoryx) alticornis*, but made special note of the fact that the specimen appeared "as heavy, but considerably shorter than type." Unfortunately there are no teeth associated with this specimen from the Barstow.

Merycodus (Paracosoryx) furlongi (Frick), U.C. no. 26795 (Furlong, 1927, pl. 26, fig. 1; Frick, 1937, p. 348), differs in having forward-tilting horn cores with longer tines, and in having a much more advanced type of ramus and lower dentition.

Neither *M. loxocerus* nor *M. hookwayi* appears to have any counterpart among recorded merycodonts. They may represent a primitive type which developed into localized aberrant forms.

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PLATES



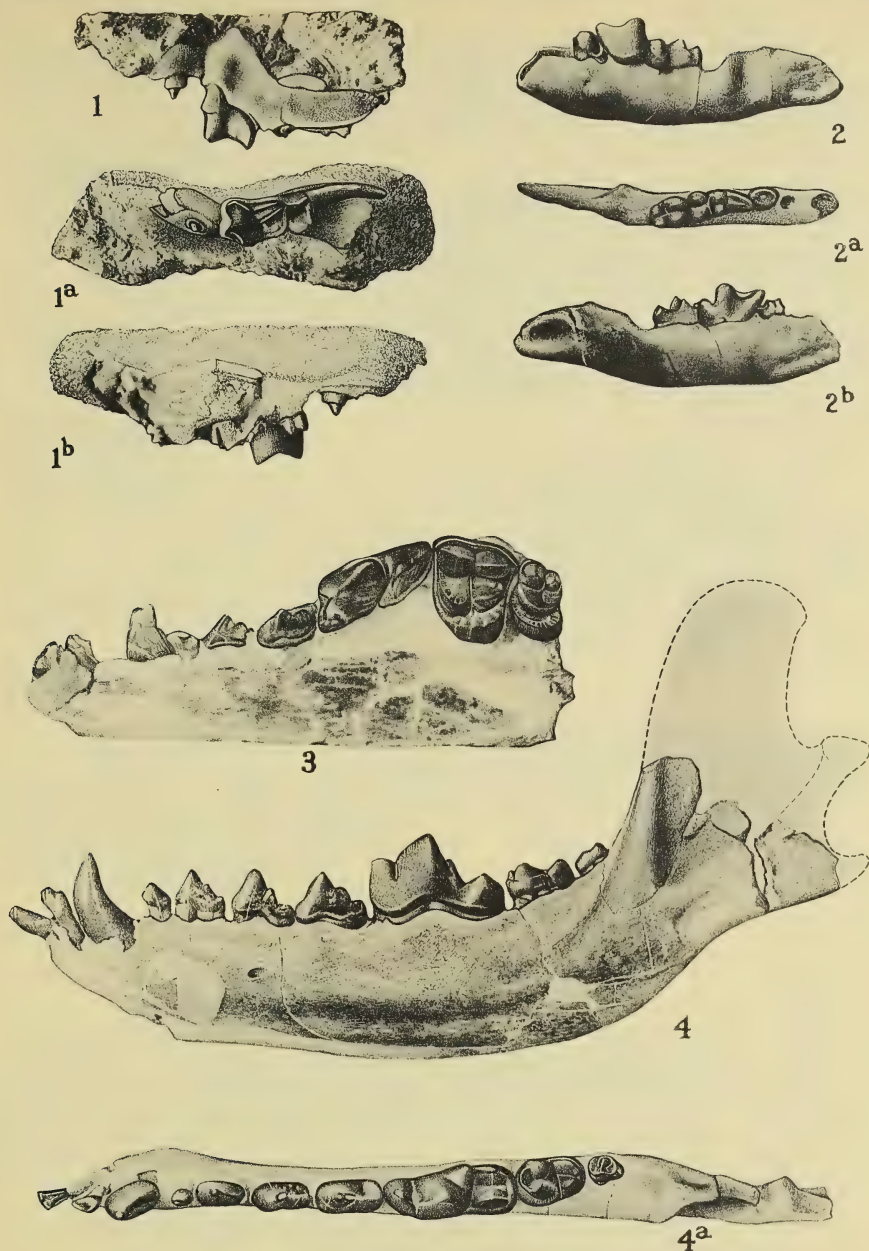
FIG. 1. View of Quarry A from the northwest. Quarry A is cut on side of hill in center of picture. Quarry C lies out of sight on back slope of same hill. Both quarries occur at approximately the same stratigraphic horizon. This horizon has been offset by minor faulting.



FIG. 2. Blasting to loosen overburden at Tonopah Quarry C. View from the east. Fossiliferous strata dip gently southward.



FIG. 3. Panorama of western slope of San Antonio Mountains, looking S. 45° W. to W. from a point 10 miles north of Tonopah, Nevada. Southern end of Big Smokey Valley lies in distance with Lone Mountain beyond. Location of Quarries A and C of Calif. Inst. Tech. Vert. Pale. Locality 172 is indicated on photograph.



FIGS. 1, 1a, 1b. *Metechinus fergusonii*, n. sp. Type specimen, no. 2817, left maxillary dentition. Fig. 1, lateral view; fig. 1a, occlusal view; fig. 1b, lingual view. $\times 2.75$.

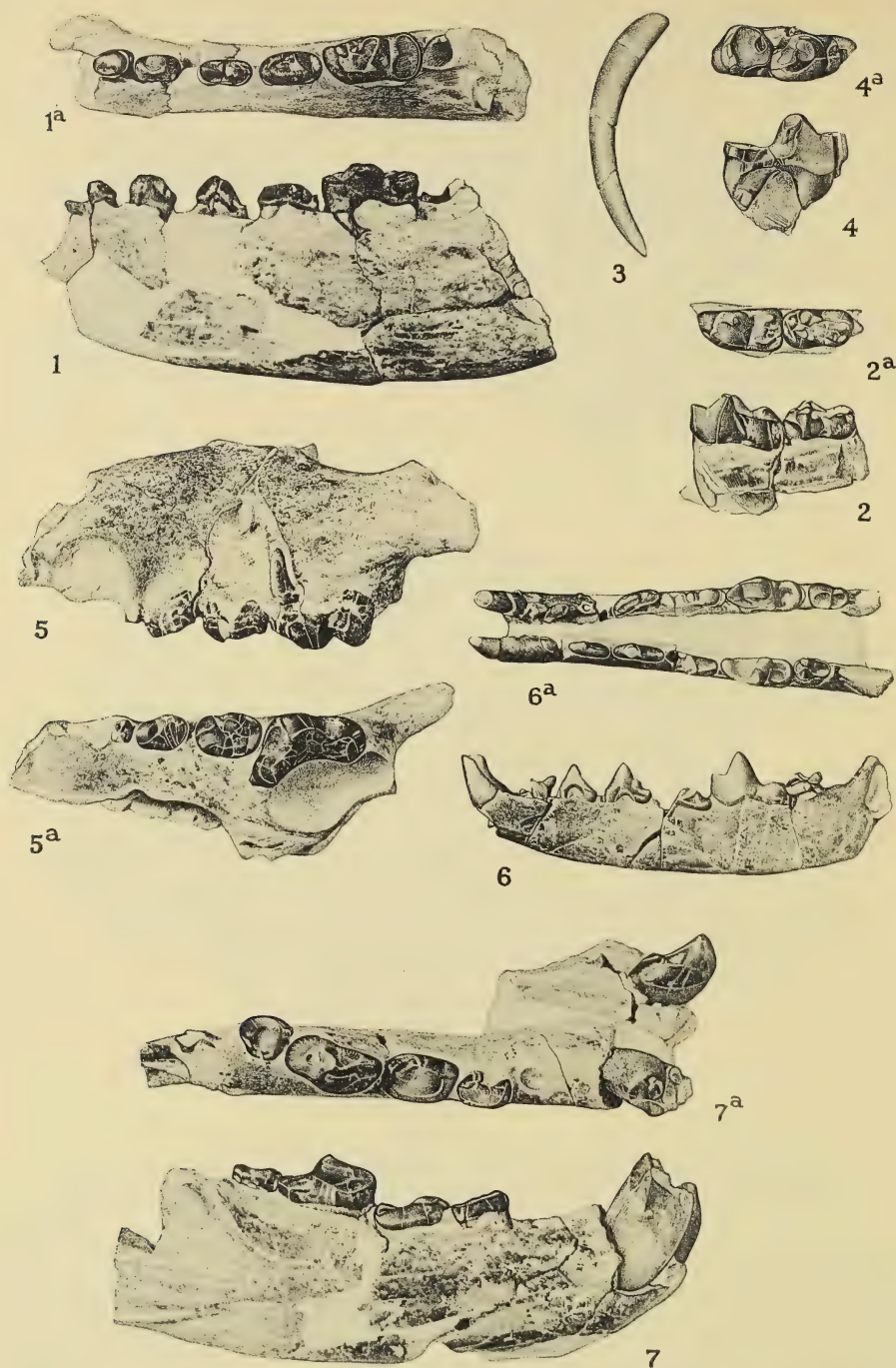
FIGS. 2, 2a, 2b. *Metechinus fergusonii*, n. sp. Type specimen, no. 2817, left ramus and dentition. Fig. 2, lateral view; fig. 2a, occlusal view; fig. 2b, lingual view. $\times 2.75$.

FIG. 3. *Tomarctus paulus*, n. sp. Type specimen, no. 1229, skull fragment with dentition, anterior teeth slightly crushed, occlusal view. $\times 1.2$.

FIGS. 4, 4a. *Tomarctus paulus*, n. sp. Type specimen, no. 1229, left ramus, ascending part restored from right side. Fig. 4, lateral view; fig. 4a, occlusal view. $\times 1.2$.

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



FIGS. 1, 1a. *Tomarctus? kelloggi* (Merriam). No. 1235, left ramus and dentition. Fig. 1, lateral view; fig. 1a, occlusal view.

FIGS. 2, 2a. *Tomarctus? kelloggi* (Merriam). No. 789, left M_1 - M_2 . Fig. 2, lateral view; fig. 2a, occlusal view.

FIG. 3. *Tomarctus brevirostris* Cope. No. 2853, canine, lateral view.

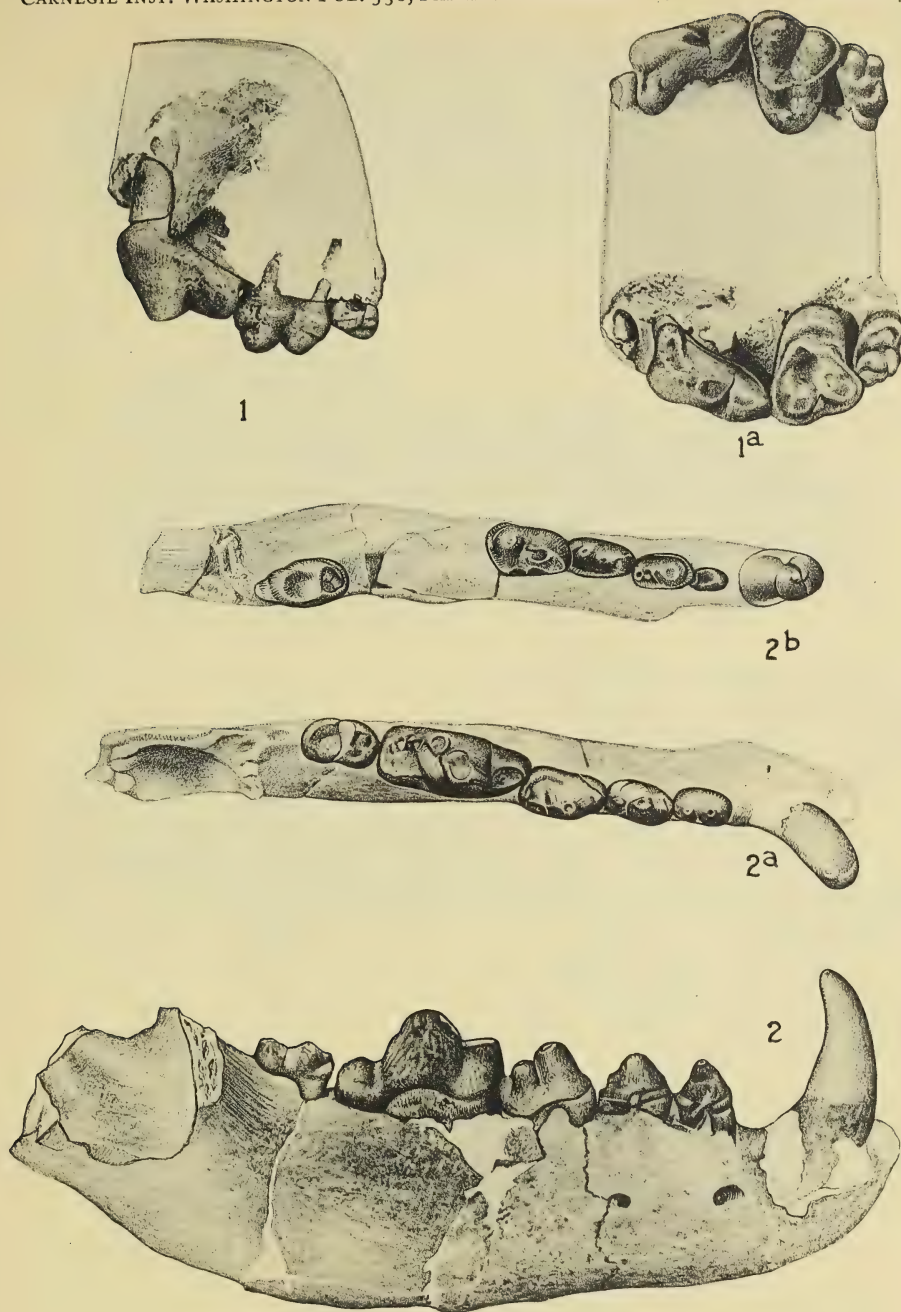
FIGS. 4, 4a. *Tomarctus brevirostris* Cope. No. 774, M_1 . Fig. 4, lateral view; fig. 4a, occlusal view.

FIGS. 5, 5a. *Brachypsalis pachycephalus* Cope. No. 1231, left maxillary and dentition. Fig. 5, lateral view; fig. 5a, occlusal view.

FIGS. 6, 6a. *Leptocyon vafer* (Leidy). No. 780, mandible. Fig. 6, lateral view; fig. 6a, occlusal view.

FIGS. 7, 7a. *Brachypsalis pachycephalus* Cope. No. 1230, right ramus. Fig. 7, lateral view; fig. 7a, occlusal view.

All figures approximately natural size



Aelurodon wheelerianus asthenostylus, n. var.

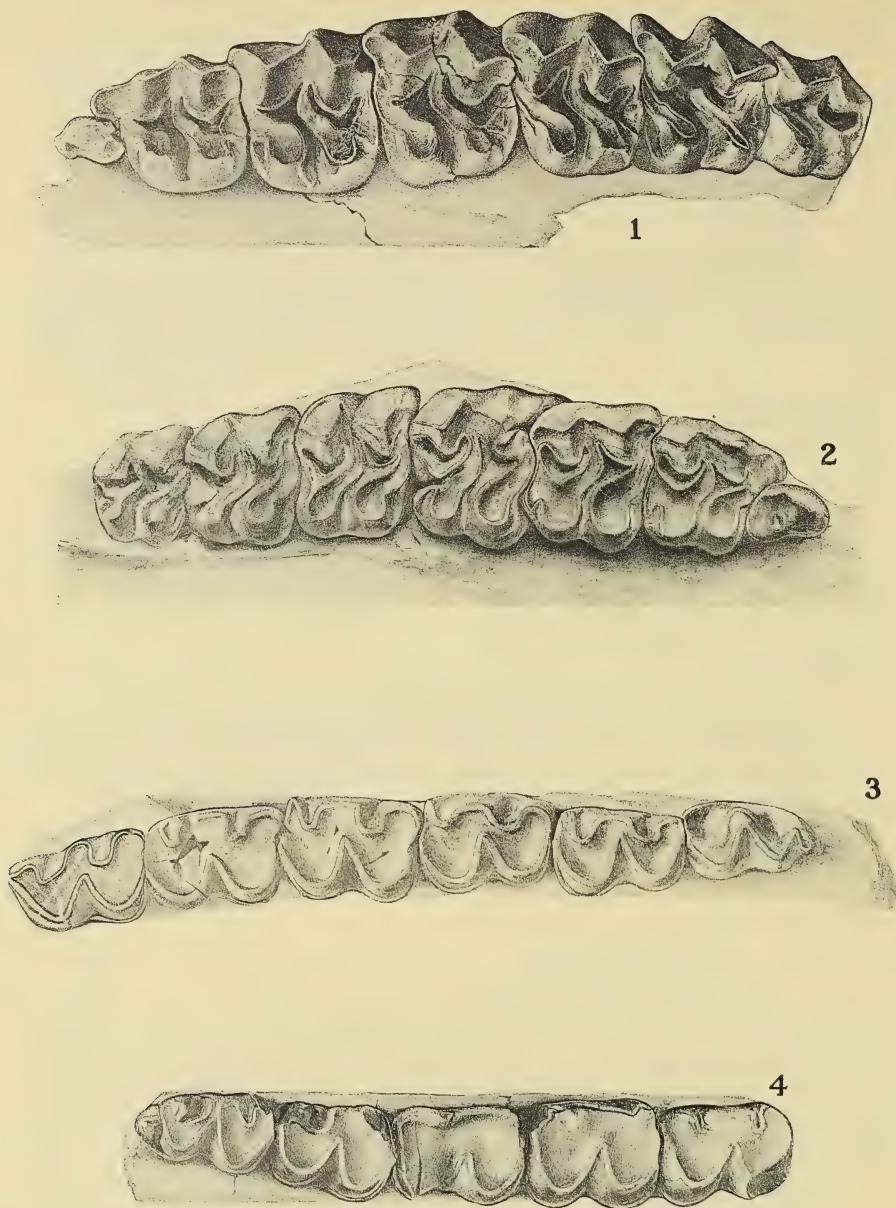
FIGS. 1, 1a. Type specimen, no. 781, maxillary with P⁴-M². Fig. 1, lateral view; fig. 1a, occlusal view.

FIGS. 2, 2a, 2b. Type specimen, no. 781, rami. Fig. 2, lateral view; figs. 2a, 2b, occlusal views.

All figures approximately $\times 0.88$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



Hypohippus near *affinis* (Leidy)

FIG. 1. No. 1404, upper dentition.

FIG. 2. No. 1401, upper dentition.

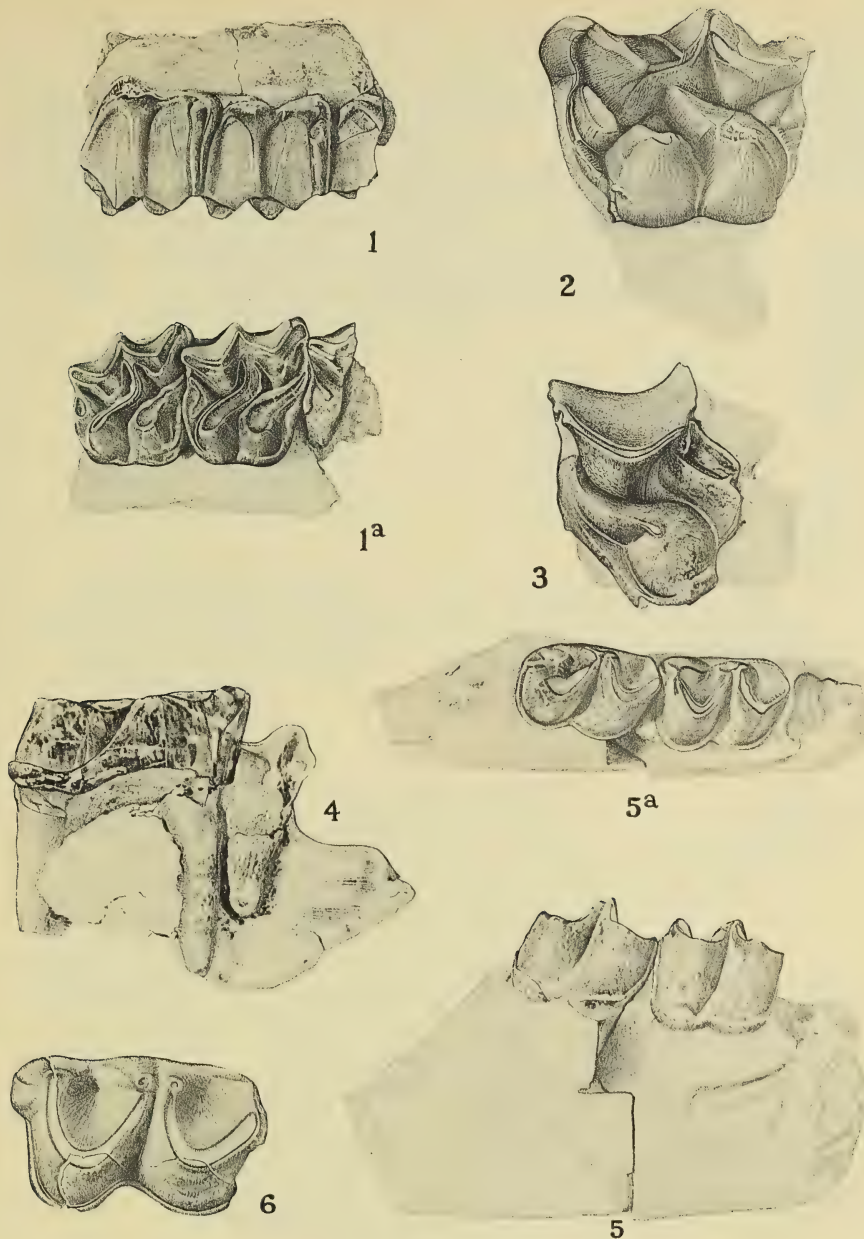
FIG. 3. No. 1880, lower dentition.

FIG. 4. No. 1881, lower dentition.

Occlusal views, $\times 0.67$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



Hypohippus near affinis (Leidy)

FIGS. 1, 1a. No. 2860, M¹-M². Fig. 1, lateral view; fig. 1a, occlusal view.

FIG. 2. No. 2845, Dm², occlusal view.

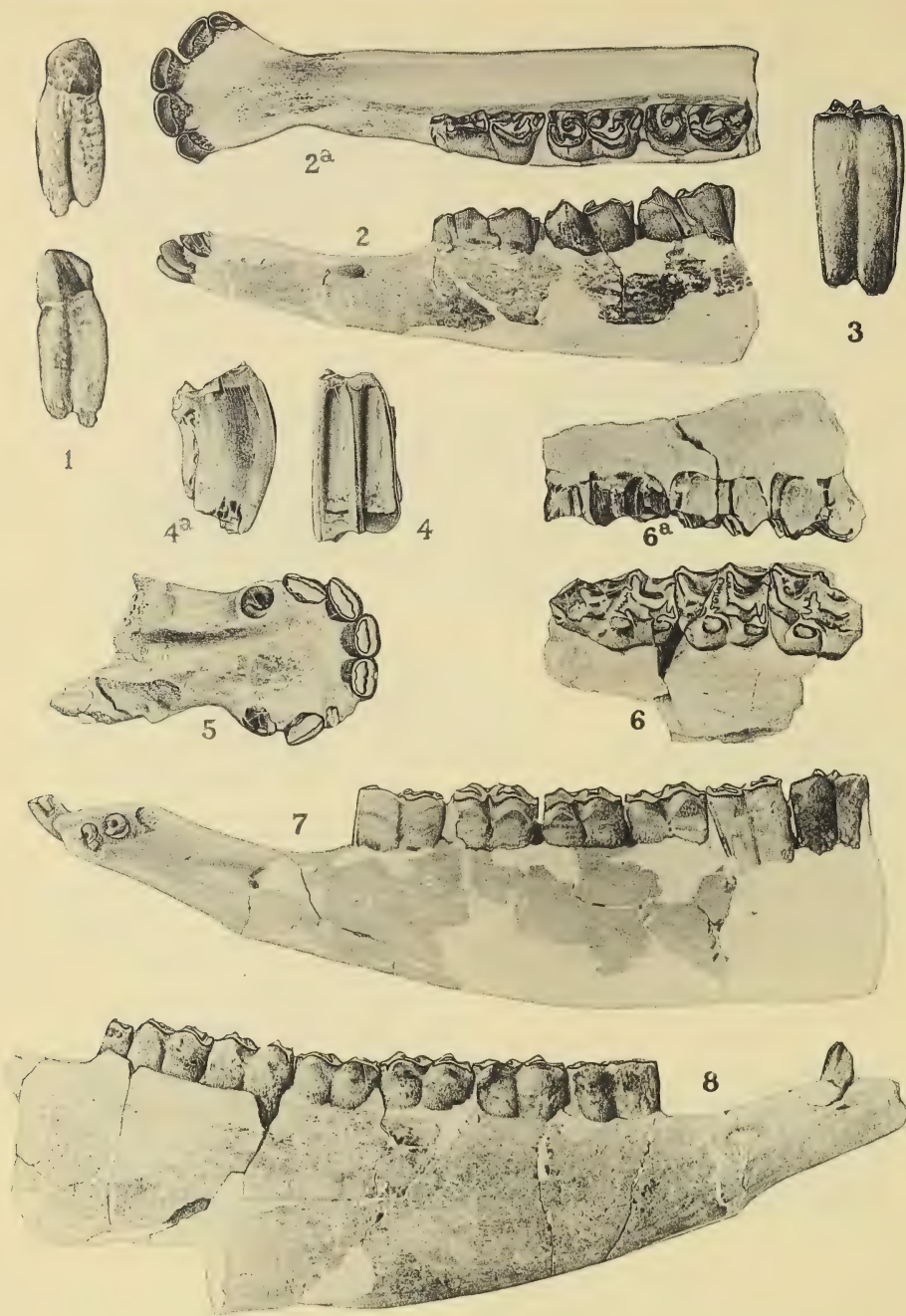
FIG. 3. No. 2846, Dm², occlusal view.

FIG. 4. No. 2847, P₁-P₂, lateral view.

FIGS. 5, 5a. No. 1878, P₃-P₄. Fig. 5, lateral view; fig. 5a, occlusal view.

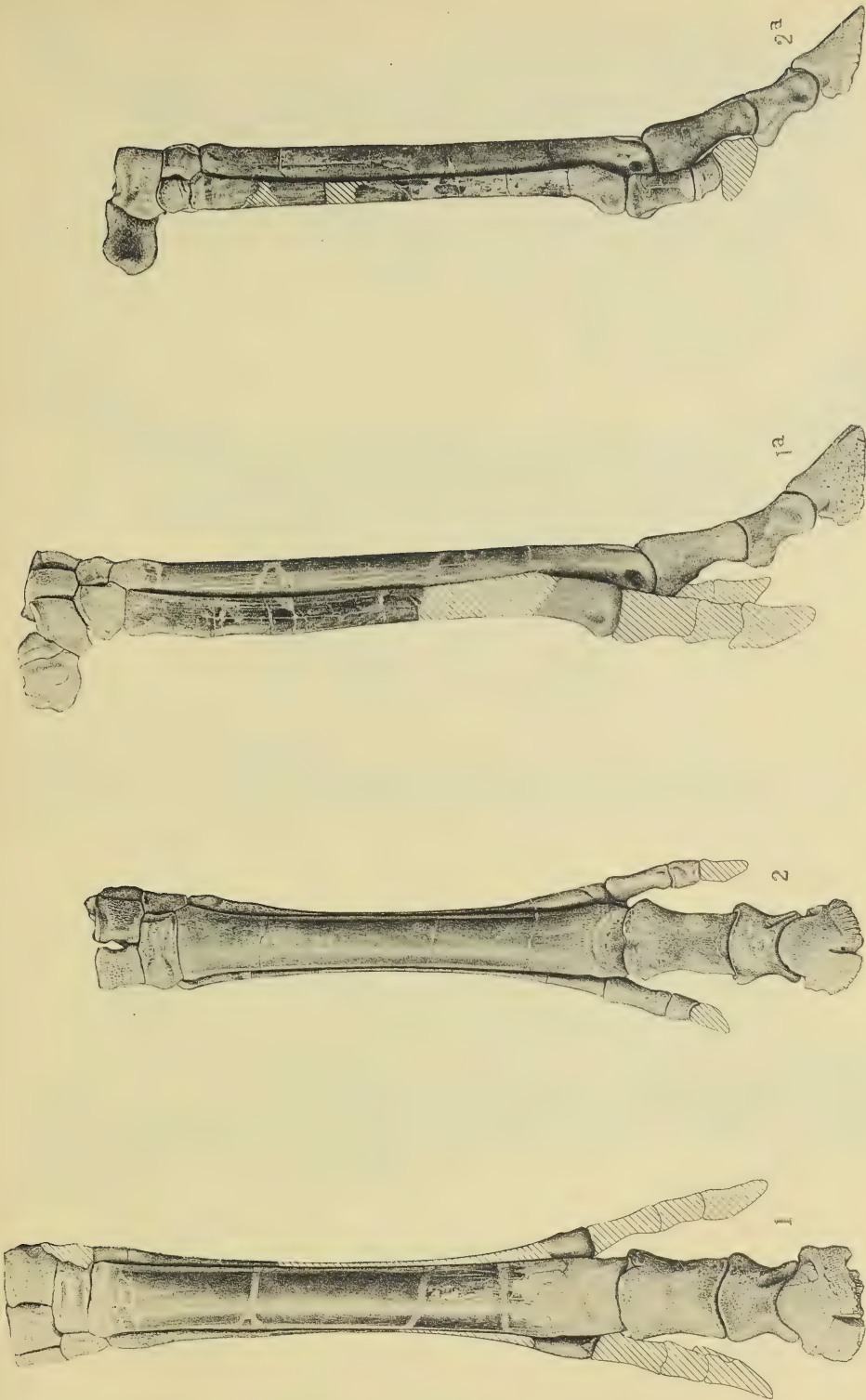
FIG. 6. No. 2848, deciduous lower molar, occlusal view.

All figures $\times 0.6$

*Merychippus calamarius* (Cope)FIG. 1. No. 2837, P_1 , lateral and lingual views. Natural size.FIGS. 2, 2a. No. 656, lower milk dentition. Fig. 2, lateral view; fig. 2a, occlusal view. $\times 0.5$.FIG. 3. No. 2862, P_4 , lateral view. $\times 0.5$.FIGS. 4, 4a. No. 2861, M^2 . Fig. 4, lateral view; fig. 4a, occlusal view. $\times 0.5$.FIG. 5. No. 2836, lower incisors and canines, occlusal view. $\times 0.5$.FIGS. 6, 6a. No. 2843, upper milk dentition. Fig. 6, lateral view; fig. 6a, occlusal view. $\times 0.5$.FIG. 7. No. 678, ramus and dentition, lateral view. $\times 0.5$.FIG. 8. No. 2834, ramus and dentition, lateral view. $\times 0.5$.

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



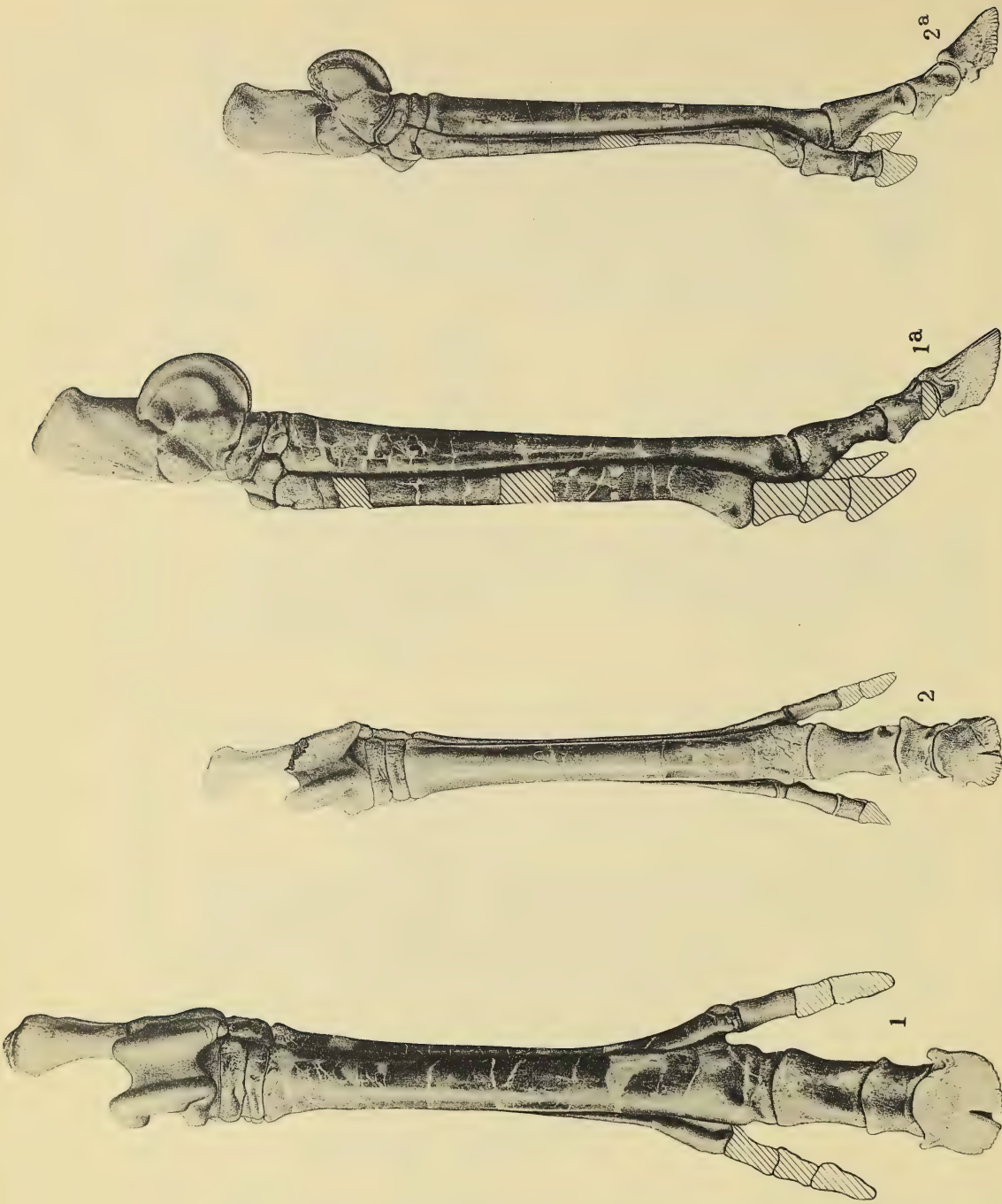
FIGS. 1, 1a. *Hypohippus* near *affinis* (Leidy). No. 2856, right manus. Fig. 1, anterior view; fig. 1a, lateral view.

FIGS. 2, 2a. *Merychippus* *calamarius* (Cope). No. 2854, left manus. Fig. 2, anterior view; fig. 2a, medial view.

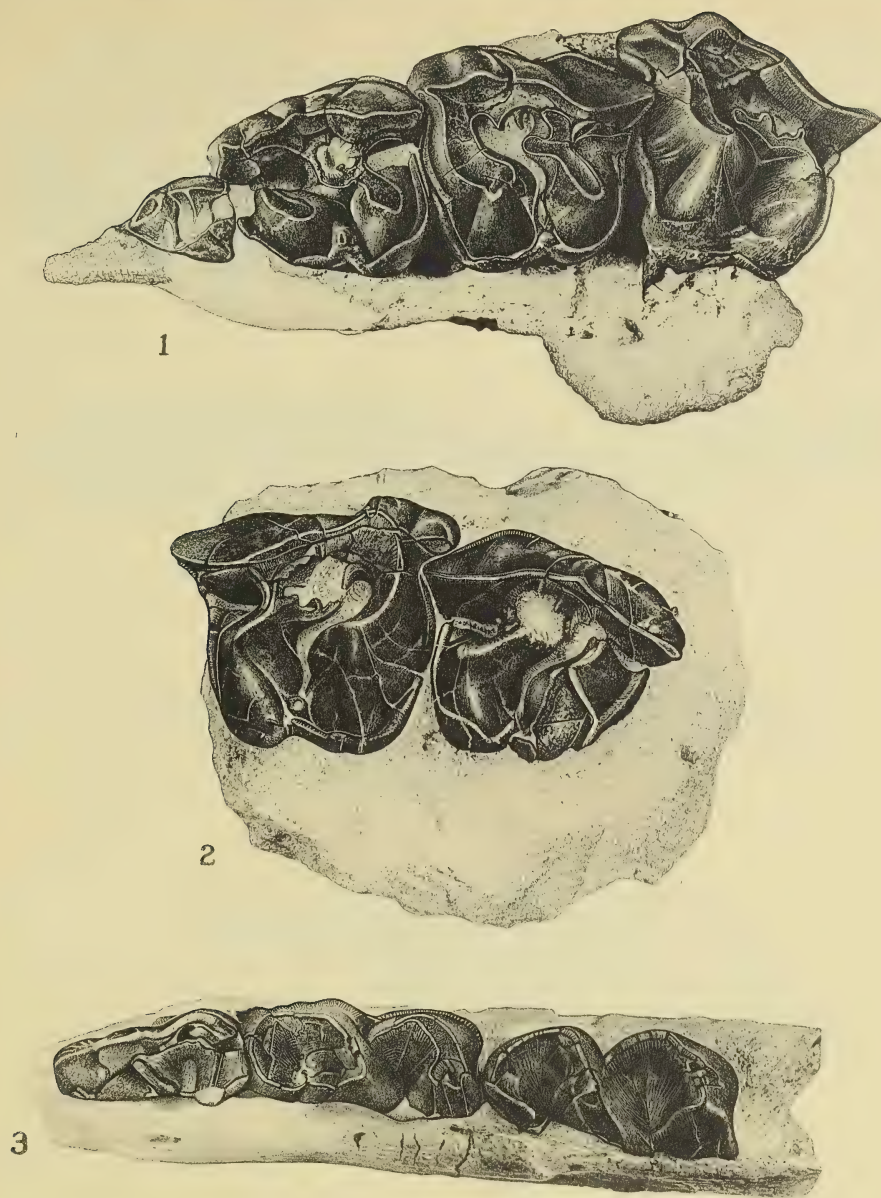
All figures $\times 0.4$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



FIGS. 1, 1a. *Hypolhippus* near *affinis* (Leidy). No. 2857, left pes. Fig. 1, front view; fig. 1a, medial view.
FIGS. 2, 2a. *Merychippus calamarius* (Cope). No. 2855, left pes. Fig. 2, front view; fig. 2a, medial view.
All figures $\times 0.33$



Aphelops? cristatus, n. sp.

FIG. 1. No. 2806, P^1 , Dm^2 - Dm^4 .

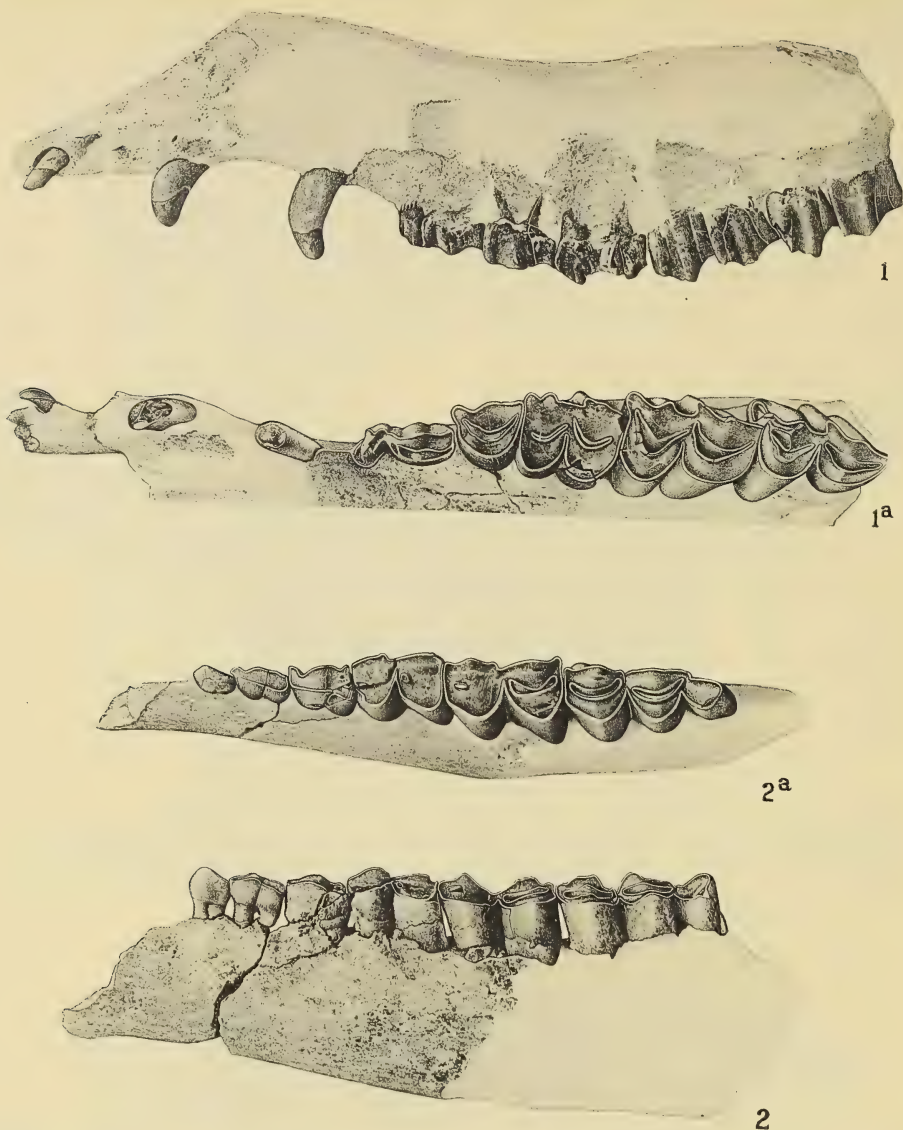
FIG. 2. No. 762, Dm^2 - Dm^3 .

FIG. 3. No. 2809, Dm_2 - Dm_4 .

Occlusal views, $\times 0.67$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada



Alticamelus? stocki, n. sp.

FIGS. 1, 1a. Type specimen, no. 1434, skull fragment with dentition. Fig. 1, lateral view; fig. 1a, occlusal view.

FIGS. 2, 2a. Paratype, no. 2819, ramus and dentition. Fig. 2, lateral view; fig. 2a, occlusal view.

All figures approximately $\times 0.5$

Calif. Inst. Tech. Vert. Pale. Coll.

Upper Miocene, Tonopah, Nevada

VI

PRELIMINARY STUDY OF THE FAUNA OF RAMPART CAVE,
ARIZONA

ROBERT W. WILSON

With four plates and one text figure

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PRELIMINARY STUDY OF THE FAUNA OF RAMPART CAVE, ARIZONA¹

INTRODUCTION

Rampart Cave lies 50 miles air line from Boulder City, Nevada, in the lower Grand Canyon of the Colorado River, and about 5 miles from Pierce Ferry. It is within the Boulder Dam Recreational Area of the National Park Service. The cave is on the south side of the river in the lower part of the Muav limestone, the first cliff-forming member of the Canyon section at this point. Rampart Cave is about 1750 feet in elevation, and at present (January 1941) it is some 580 feet above the shores of Lake Mead. Before the construction of Boulder Dam, the Colorado River was approximately 915 feet in elevation at the cave.

Rampart Cave is visible from the Colorado River (plate 1), and apparently its existence was known to boatmen on the river, but it was not until the early summer of 1936 that its scientific importance was realized. At that time Willis Evans, junior foreman in the National Park Service, visited the cave and recognized the fact that its floor was composed of ground-sloth dung. Soon after this discovery, National Park Service officials had two test pits dug in the floor of the cave. The larger of these, pit B, is about 200 cubic feet in volume; the other, pit A, is considerably smaller. From these two pits came several hundred determinable elements of fossil vertebrates, more than half of them of the ground sloth *Nothrotherium*. No further excavation has been attempted since that time, for it was felt that additional work at the cave should await the acquisition of sufficient staff and equipment to do a thorough, painstaking piece of work. The specimens are at present in the collections of the museum in the National Park Service headquarters at the Boulder Dam Recreational Area, Boulder City, Nevada. Part of the collection is on public exhibit.

A preliminary announcement of the discovery was made by Senior Geological Foreman Edward T. Schenk (1936, p. 399). Later, samples of the dung were analyzed for their floral content by Lauder milk and Munz (1938). In the early part of 1939, the writer was appointed collaborator by the National Park Service for a period of several months in order to assist in the identification of fossil vertebrates in the collections at Boulder City. The present paper is one result of the work. No attempt is made at exhaustive treatment, since that can be done much better when excavation of Rampart Cave is completed.

ACKNOWLEDGMENTS

The author wishes to take this opportunity to thank the National Park Service, originator of the project, for cooperation in numerous ways, and for permission to publish the results of the work. Special acknowledgments for many

¹Published by permission of the Director, National Park Service.

courtesies and much stimulating discussion are extended to Guy D. Edwards, supervisor of the Boulder Dam Recreational Area, and the members of his staff with whom I came into direct association: Robert H. Rose, park naturalist; Russell K. Grater, now park naturalist at Zion National Park; and Bert Long, junior park naturalist. Particularly do I wish to thank Edward T. Schenk, senior geological foreman, who bore the brunt of most of my requests, and with whom I spent a number of instructive days both in the field and at Boulder Dam headquarters. The illustrations are all from negatives in the collections of the National Park Service, Boulder Dam Recreational Area, and are published by permission of the Service.

OCCURRENCE OF MATERIAL

Rampart Cave is about 150 feet from the portal to the back wall where the test pits were excavated, but the total length of the cave is nearly double that figure. Throughout most of its length it is less than 20 feet wide, and at the widest point it is not much more than 30 feet. According to a map made by the Park Service (fig. 1), the cave has an area of 4700 square feet. The floor presents a nearly even surface of dung, which in places is 6 feet or more

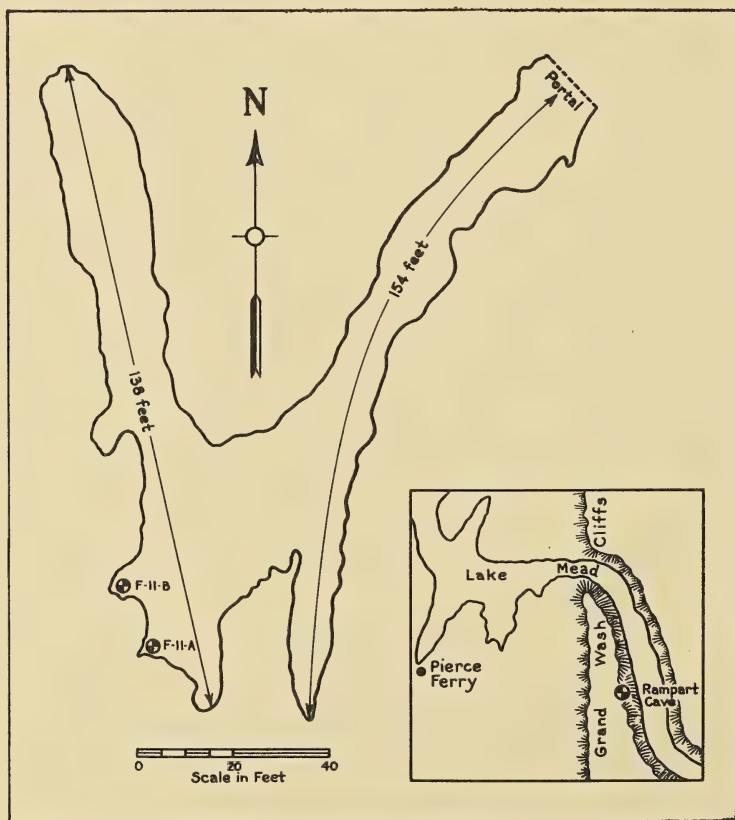


Fig. 1. Sketch map showing location of Rampart Cave, and floor plan of cave

in thickness. Schenk estimates about 2000 square feet of dung, which is certainly a minimum figure. In view of the small size of the test holes, it is evident that a great quantity of fossil material remains to be obtained, and Rampart Cave should prove to be one of the more important "dry cave" accumulations. Because of the dung, the roof of the cave is now low in many places (pl. 2, fig. 1). A sharp and penetrating odor is noticeable at once as one enters the cave. This is probably due chiefly to the large quantity of fine material in the dung, which fills the air on the slightest disturbance. The floor of the cave has a very dry, springy feel under foot, and a somewhat hollow sound. Apparently, little sediment is mixed with the dung.

The fauna obtained from the test pits is as follows:

Gopherus agassizii
Sauromalus probably ater
Aves
*Nothrotherium shastense
Marmota flaviventris cf. engelhardti
Lepus near californicus
Bassariscus astutus
Felis concolor?
Lynx species
Oreamnos *harringtoni
Ovis species
*Equus species

*Extinct.

Among the specimens already obtained, the proportion of non-sloth elements increases decidedly with depth. In the first 3 feet in pit B, the *Nothrotherium* elements probably outnumber the others about ten to one. Below 3 feet, the sloth elements appear to be outnumbered by the non-sloth elements. Among the last hundred or so specimens catalogued, which are those obtained from the greatest depth, the ratio of *Nothrotherium* to other elements is only one to three. In view of the small size of the test pits, however, it would seem reasonable to suppose that the increase in non-sloth elements in the lower 2 feet of pit B, and the relative decrease in sloth at that depth, is due largely to chance local distribution. On the other hand, there may be a slight change with depth, especially in regard to animals such as *Marmota* and *Oreamnos harringtoni*. Only subsequent excavation can establish this point with certainty. The specimens near the bottom do not seem any older in physical appearance. The finding of turtle and chuckwalla remains at 5 feet would preclude, on present evidence, the assumption of any distinct climatic change during occupancy of the cave.

ENVIRONMENT OF THE RAMPART CAVE FAUNA

Laudermilk and Munz after study of the plants in the dung of *Nothrotherium* concluded that "when the ground sloths inhabited Rampart and Muav Caves,²

²Muav Cave, in the same general vicinity as Rampart, is similar to it, but the floor of the cave is disturbed and animal bones are rare.

the flora and presumably the climate were essentially the same as those of the region today." The climate in this area today is very hot and arid; the flora and fauna are of the Lower Sonoran zone. The cave reptiles apparently offer the same evidence as the flora in regard to climatic conditions.

Among the mammals, *Lepus*, *Felis*, *Lynx*, *Bassariscus*, and *Ovis* are all genera that are represented by species in the region today. Although it is probable that the cave forms are identical with indigenous species, the specimens available are not complete enough to exclude entirely the possibility that they are to be identified with forms living under different climatic conditions.

The foreign element is represented by *Nothrotherium*, *Oreamnos*, *Marmota*, and *Equus*.³ The presence of *Nothrotherium* and of *Equus* seems compatible with the environment as suggested by the flora. The long, coarse hair of the sloth, however, may indicate that *Nothrotherium* was not entirely at home in the pictured environment. The genus was certainly a habitual cave dweller, and almost all known North American occurrences are from cave deposits.

The remaining two mammalian genera, *Marmota* and *Oreamnos*, seem entirely out of place in a Lower Sonoran life zone. Marmots are at present absent from Arizona, and do not occur south of the Colorado River except in the Rocky Mountain region of Colorado and New Mexico, the nearest records being from central Nevada and southern Utah. They are generally confined to Transition and higher life zones. The living mountain goat is at home in the mountainous region extending northward from Washington, Idaho, and Montana toward and up the Pacific Coast to Alaska. It occupies the Arctic-Alpine zone. The geographic range of both genera, however, was evidently greater in the Pleistocene. Thus, Pleistocene *Marmota* is recorded at least as far south as Sonoita, Santa Cruz County, Arizona, and probably into Mexico. Rampart Cave is the most southern recorded occurrence of *Oreamnos*, but undescribed specimens are known from Mexico. Though the isolated nature of the Great Basin ranges and the presence of the Colorado River athwart the Colorado Plateau offer formidable climatic and geographic barriers to migration into the region today, both *Marmota* and *Oreamnos* may have spread during a cooler period of the Pleistocene. Their increased range would gradually shrink with the return of warmer conditions. The topographic features of the lower Grand Canyon with its towering cliffs and numerous talus slopes offer such ideal homes that these genera might have been able to persist in this area after the climatic factor was very unfavorable. Bailey (1936, p. 161), discussing the eastern Oregon range of *Marmota flaviventris avara*, says, "Over wide areas of valley and prairie they are entirely absent, but generally in the rimrock, cliffs, canyon walls, and lava fields are more or less common. Most of their range lies in Upper Sonoran and

³Wild burros range near the cave today, but the cave record of the genus is based on an incomplete phalanx found under nearly 5 feet of dung.

Transition Zones, but little choice of habitat is shown other than safe cover of rocks and a satisfactory food supply."

Since the species of *Oreamnos* present at Rampart Cave is extinct, it might be postulated that *O. harringtoni* differs from Recent *Oreamnos* in habitat, and even is a desert goat analogous to the desert mountain sheep. That this hypothesis is correct, however, hardly seems probable. The type material of *O. harringtoni* is from Smith Creek Cave in the Snake Range, approximately 34 miles north of Baker, White Pine County, Nevada. This locality is at an elevation of 6200 feet and considerably farther north than Rampart Cave, and the goat is associated with pika and numerous marmot specimens. In other words, Smith Creek Cave apparently has a high life-zone fauna. Thus it is unlikely that the Arizonan goat was a desert type in the same sense that *Ovis canadensis nelsoni* is a desert sheep.

There are several serious objections to the supposition that the climate at Rampart Cave was much cooler than today at any time during occupancy of the cave. Among them are the evidence of the plant remains, and the association of certain reptiles with mammals to the very bottom of pit B.

In summary, the environment at Rampart Cave during the period of accumulation of fossil remains seems to have been essentially like that of today. The climate may have been somewhat cooler, but not enough so to affect the flora to a noticeable degree. The presence of marmot and goat is best explained perhaps by the favorable topographic conditions, which for a time overshadowed the unfavorable climatic state. In this connection, it should be pointed out that owing to the considerable topographic relief in the Grand Canyon area, life zones range from Lower Sonoran at the river to Transition on the Colorado Plateau. The relatively mobile goat need not have habitually occupied the area immediately surrounding the cave, but may have lived in cooler environs during the summer months. Perhaps, also, it should be stressed that the explanation offered for the presence of *Marmota* and *Oreamnos* is mainly an attempt to reconcile various lines of evidence.

Since the body of this paper was prepared, the writer has received a written communication from Russell K. Grater, park naturalist at Zion National Park. His interpretation of the fauna and flora differs somewhat from the one given here, and from that of Lauder milk and Munz. The author takes full responsibility for errors in the following attempt at summarization of Grater's views:

Evidence drawn from the presence of certain reptiles fails to add much weight to the plant evidence. Chuckwalla specimens have been collected in the Upper Sonoran zone at Grand Canyon, and it may be seriously questioned whether the desert tortoise had the ability to climb to the cave entrance. This form possibly was carried in and eaten by some enemy. Further, it is doubtful whether either goat or marmot among the mammals was a species tolerant, willingly or not, of arid conditions. It is believed that the life zone at the cave must have been Upper Sonoran with a luxuriant vegetational cover. Substantiating this statement are vast quantities of travertine throughout the region, which

indicate many springs and seeps. Running water was much more abundant than now. Side canyons near Rampart Cave supported a heavy cover of plants which were much the same as those that now grow at around 3000 feet in the upper Grand Canyon. The yellow pine zone occurred chiefly below the rim of the Canyon. The rim was a region of cold winters and heavy snows.

AGE OF THE RAMPART CAVE FAUNA

In the course of time, a satisfactory chronology for late Pleistocene--post Pleistocene faunas probably will be developed. At present, however, exact determination of the age of the Rampart Cave fauna is hardly possible. The physical features of the cave deposit and its fauna give a superficial impression of material a few hundred years old. The occupation of the cave by extinct genera and species, however, and by an animal that no longer lives in the region, is *prima facie* evidence of antiquity. Except possibly *Equus*, these animals must have been rather common, in view of the small size of the test pits. It is reasonable to assume that the deposit is post-Pleistocene in age. A rough estimate might be between a few thousand and 20,000 years.

The age of the similar occurrence at the near-by Gypsum Cave, Nevada, has been estimated at 10,000 years more or less (Harrington, 1933, pp. 171, 188). The *Nothrotherium* dung from this cave, however, has a flora "found today only at elevations 3000 feet or more higher than Gypsum Cave. In other words, at the time when ground sloths, and perhaps man, inhabited Gypsum Cave, the climate was distinctly more humid than it is today" (Laudermilk and Munz, 1934, p. 37). Thus a comparison of the two floras indicates a more recent age for the Rampart Cave fauna (but see Grater's opinion given above). Whether it actually is younger may well remain an open question at present. There does not seem to be any significant difference in the faunas as regards geological age, unless the presence of marmot and goat at Rampart indicates after all a considerably cooler climate than at Gypsum Cave. This, of course, is the reverse of the evidence offered by the floras.

DESCRIPTION OF FAUNA

Gopherus agassizii (Cooper)

Scattered remains of the desert tortoise were found at various depths in test pit B. Several specimens were obtained at a depth of 5 feet. Included in the tortoise material are: a skull, no. B403; a mandible, no. B424; and fragments of the shell, some still covered by the horny shields. These specimens are in the collections of the National Park Service at Boulder City, Nevada. The species seems to be identical with the desert tortoise, *Gopherus agassizii*.

Sauromalus probably *ater* Duméril

The known lizard specimens include, among others: two incomplete skulls, one distinctly larger than the other, nos. B404, B430; a mandible, no. B406; and a

left and a right ramus, nos. B407, B429. At least the larger of the two lizards, as represented by nos. B404 and B406, is probably the chuckwalla, *Sauromalus ater*. These specimens were found at a depth of 5 feet. The smaller lizard skull, no. B430, is an iguanid, and may be a young chuckwalla.

Desert tortoises and chuckwallas are apparently in valid association with the mammals. The presence of these reptiles would naturally seem to indicate a warm, arid climate. In the final analysis, the less adaptable forms of life should be more important in reaching climatic conclusions than the mammals.

Aves

Various fragmentary specimens of birds, some at least indicating an animal of relatively large size, have been obtained from the cave. Depths range from 2 feet 6 inches to 4 feet 9 inches. The types represented have not been determined.

Nothrotherium shastense Sinclair

(Plate 3)

In the two test pits opened, *Nothrotherium* is represented, as would be expected, by the greatest number of skeletal elements. All specimens from the smaller pit, A, are of this animal, and more than half of those from pit B. It is difficult to estimate the number of individual elements because of the presence of numerous epiphyses, fragments of vertebrae, rib fragments, and the like, most of which have been catalogued as separate specimens. A reasonable estimate would be 200 separate skeletal parts. At least eight, presumably more, individual animals are represented by these elements, ranging from very immature to fairly adult sloths. Practically all the *Nothrotherium* elements, however, are of young individuals, with fully adult skeletal parts rare or absent. For this reason, most of the elements lack one or another of their epiphyses, or are smaller than those from Rancho La Brea described by Stock (1925).

Various soft parts, rarely found preserved, are rather common. These include dung, hide, hair, cartilage--especially intervertebral pads--a trachea, and undetermined tissues possibly relating to the sloth.

The skull is known by one nearly complete cranium, no. B13, and mandible, no. B1 (pl. 3, fig. 1); the posterior part of a second cranium, no. B85; a right maxillary with cheek teeth ²⁻⁵, no. B4; a left ramus with ₄, no. B154; a mandible with cheek teeth of a very young individual, no. B386; and a number of skull fragments and isolated cheek teeth. Several hyoid bones have been identified tentatively.

Cranium and mandible nos. B13 and B1 offer the best opportunity to determine the species of *Nothrotherium* present. The cranium lacks the right malar, neither zygomatic process of the squamosal is complete, and there is some damage to the pterygoid bullae. Most of the cheek teeth are more or less

imperfect or missing. The crowns of right 4 and left 2 and 4 are gone, although the deeper parts lying in the alveolar sockets are still present. In the mandible, the upper parts of the crowns of right 2 and 4 are missing, and these same teeth on the left side are completely gone. Otherwise the skull is nearly perfect, including the seldom found premaxillaries.

Skulls of *Nothrotherium shastense* from Rancho La Brea, as described by Stock, and particularly L.A.M. 1800-11, are larger than no. B13. The latter may have more nearly the dimensions of *N. shastense* from Aden Crater, New Mexico (Lull, 1929). In comparison with Rancho La Brea crania, the Rampart Cave specimen has swollen parietals that are high relatively to the frontals. The malar is rather light and slender. The most noticeable difference in the malar of no. B13 is the less rapid tapering of the ventral prong or process. The postpalatine notch is very acute, and reaches in front at least to the posterior border of the last cheek tooth. In the Rancho La Brea specimens, the position of the notch is "well posterior to the position of the fourth upper cheek-tooth" (Stock, 1925, p. 44). The notch may be less acute. The broad groove extending diagonally across the pterygoid bullae may be less developed in no. B13 than in individuals from Rancho La Brea.

No premaxillaries from Ranch La Brea have been available for description. Those in the Aden Crater specimen are somewhat obscured by the soft parts present. The premaxillaries in the Rampart Cave skull are roughly Y-shaped. The posterointernal fork is slender and straight. The posteroexternal branch is heavy, curves outward and upward, and is expanded anteroposteriorly in lateral view. The anterior part of the premaxillary beyond the anterior border of the incisive foramen is longer than the posterior part. Anteriorly, the tips of the premaxillaries end in small, somewhat rounded knobs.

The principal difference between the mandible of no. B1 and that figured by Stock is in the angle. In the Rampart Cave form, the angle is heavier viewed laterally. Moreover, it is not inflected to the extent of forming an inner shelf.

The cheek teeth in the superior dentition of no. B13 seem to be more closely spaced than in L.A.M. 1800-11. No differences were observed in the lower dentition.

Notwithstanding the skull differences noted, the Rampart Cave species is very probably *Nothrotherium shastense*. Many minor characters mentioned by Stock are present. Individual or age variation would account largely for the differences. The somewhat smaller size seen throughout the sloth material from the cave is probably due to the high, almost exclusive, proportion of young individuals. On the other hand, *Nothrotherium shastense* of Rancho La Brea and the caves of northern California is removed in time and province from the sloth of the dry caves of the Southwest. Hence, there are grounds for believing that when more specimens become available, the latter may prove to be a distinct species.



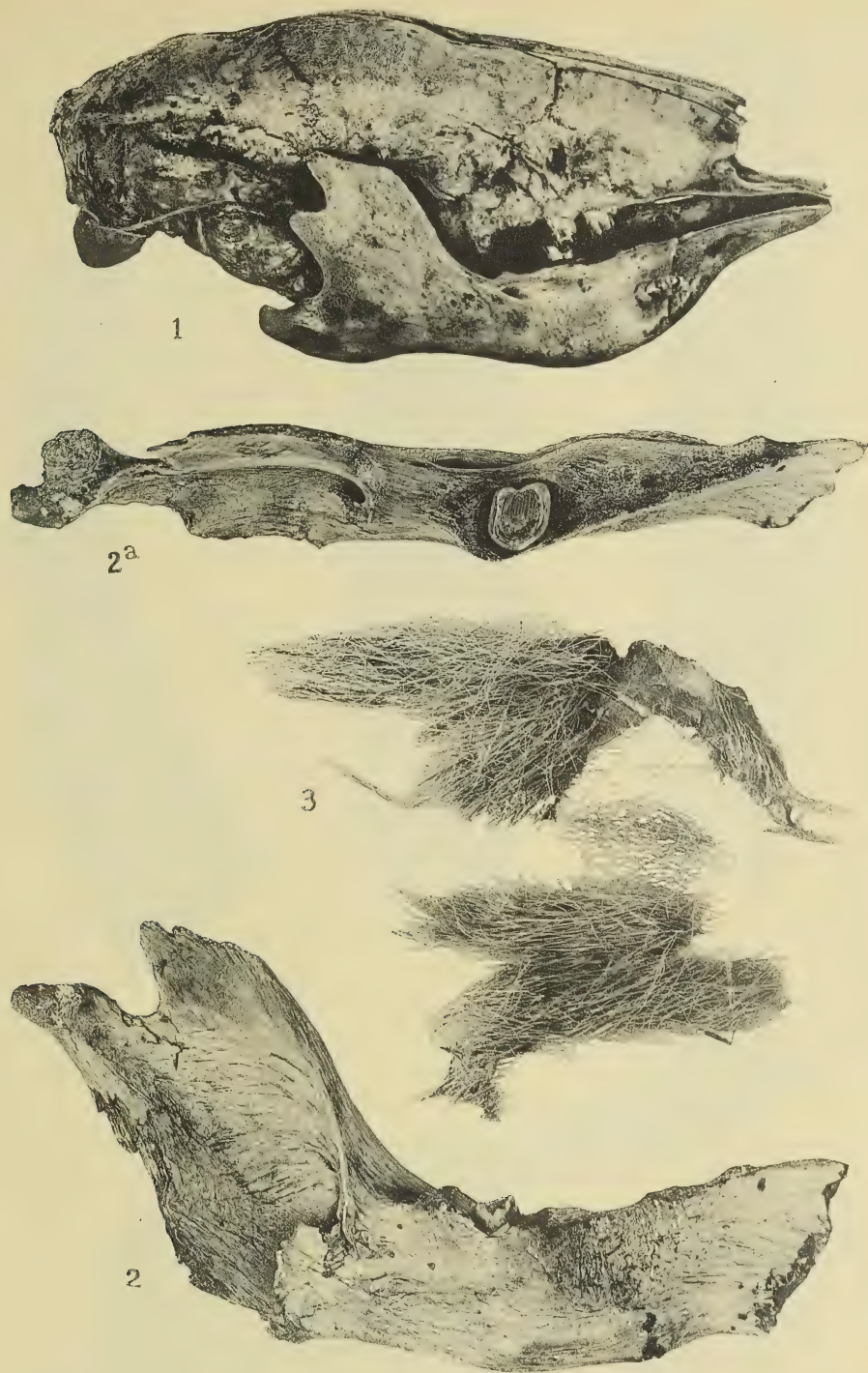
View of Rampart Cave, Arizona, taken from Lake Mead. Arrow shows entrance to cave, in Muav Limestone in wall of the lower Grand Canyon.



FIG. 1. Interior view of Rampart Cave, Arizona, showing low ceiling, and floor of ground-sloth dung.



FIG. 2. Entrance to Rampart Cave, Arizona. The gate is a bar to the "pothunter," and a precaution against the fire hazard caused by the well intentioned but careless visitor.



Nothrotherium shastense Sinclair

FIG. 1. Skull, no. B13, and mandible, no. B1, lateral view. \times approx. 0.35.

FIGS. 2, 2a. Left ramus with α , no B154. Fig. 2, medial view; fig. 2a, dorsal view. \times approx. 0.7.

FIG. 3. Fragment of hide and hair.

Coll. Mus. Boulder Dam Recreational Area

Rampart Cave, Arizona



FIGS. 1, 1a. *Oreamnos harringtoni* Stock. Left manus, no. B349. Fig. 1, anterior view; fig. 1a, posterior view, showing splints. \times approx. 0.8.

FIG. 2. *Oreamnos harringtoni* Stock. Horn sheath, no. B348, lateral view. \times approx. 0.6.

FIG. 3. *Oreamnos harringtoni* Stock. Horn sheath, no. B278, lateral view. \times approx. 0.6.

FIG. 4. *Ovis* species. Horn sheath, showing damage by solution (?), no. B400, lateral view. \times approx. 0.75.

Vertebrae and ribs are quite numerous. Vertebrae for a complete cervical series are present, together with some thirty complete or fragmentary thoracics, and a few lumbar, sacral, and caudal vertebrae. A number of hemapophyses have been obtained. The ribs and rib fragments are almost entirely costal. A manubrium and several other sternal segments are present.

Elements of the feet and hands, especially metapodials, are relatively rare, and many elements of these parts are still unknown from the cave. Proximally, however, the appendicular skeleton is represented by specimens of practically all elements, although few are complete.

One specimen of *Nothrotherium*, a left ramus, no. B154 (pl. 3, figs. 2, 2a), perhaps deserves some comment. The only cheek tooth in the jaw is the posterior one, 4. No alveoli for the other two teeth are present, although the bony rim of the alveolar border rises somewhat above the general level of the superior surface of the horizontal ramus. The jaw is obviously abnormal, since all three cheek teeth are normally present even in extremely young individuals, and teeth of persistent growth are characteristic of the sloths. Either the anterior cheek teeth were never present, or they fell out because of a diseased condition of the jaw and the alveolar pits were filled with bone. Several features of the jaw suggest that the former explanation is much more likely. The jaw of no. B154 is relatively shallow as compared with no. B1, and probably smaller, but apparently not especially immature.

Marmota flaviventris cf. *engelhardti* Allen

A number of marmot specimens were excavated from pit B at a depth of from 3 to 5 feet. The principal specimen, no. B402, is a rather complete skull without lower jaws, but with cheek teeth broken out and otherwise defective. Another, no. B329, is the medial part of a skull with right P⁴-M³ and incomplete left P⁴-M³. In addition, a number of vertebrae, mostly from the cervical region, and various limb bones have been obtained.

Characters of the skull indicate that the material should be referred to *Marmota flaviventris*, the common species of western United States. Racially, the Rampart Cave form is close to the subspecies *parvula* and *engelhardti*. Skull no. B402 is comparable in measurements with specimens of the latter, which is somewhat larger than *M. f. parvula*. This agreement is to be expected perhaps, since *M. f. engelhardti* inhabits the Colorado Plateau, and *parvula* is a Great Basin race.

Marmots are common in the Smith Creek Cave fauna of central eastern Nevada, where they are associated with topotype material of *Oreamnos harringtoni*. Specimen B402 is smaller than the average skull from Smith Creek Cave, but several specimens agree in size and other characters. Perhaps the same subspecies of marmot inhabited both localities, but the evidence at present is inconclusive, if indeed it does not point to distinct races.

A fossil record of *Marmota flaviventris* as far south as Sonoita, Arizona, already has been mentioned. Today, not only are marmots absent from the area immediately adjacent to Rampart Cave, but they are also unrecorded from the neighboring high mountain ranges of southern Nevada, such as the Charleston Mountains, which would seem to offer a favorable environment for them. E. Raymond Hall states, however (written communication), that *Marmota flaviventris* occurs in kitchen-midden deposits from northern Arizona, and in a cave in the Providence Mountains of California. The associated faunas are similar to those found in the same areas today. He is of the opinion that in early Recent time *M. flaviventris* ranged somewhat farther south than it does now.

Lepus near californicus Gray

A single specimen of *Lepus* has been obtained, no. B368, a right ramus with complete dentition. It was found at a depth of 4 feet 8 inches. This specimen cannot be distinguished from ram of *L. californicus*. The subspecies *L. c. deserticola* ranges throughout the Sonoran zone in the vicinity of the Grand Canyon. It has been stated that it does not occur in the Canyon, but this presumably refers to the part within the Grand Canyon National Park.

Bassariscus astutus (Lichtenstein)

Two specimens of the bassarisk or ring-tailed cat are in the collection from Rampart Cave. One, skull (with jaws) no. Z12, was obtained from a pack-rat nest on the surface of the cave floor. This specimen may be Recent in a strict sense, for these cave- and cliff-dwelling animals are common in the Upper and Lower Sonoran zones of the Canyon today. The Recent bassarisk from the area is *B. astutus nevadensis*. Specimen Z12 is certainly to be referred to *B. astutus*, and probably to the local race as well. The second individual, no. B405, represented by a mandible, was found in pit B at a depth of 5 feet, and hence is in undoubted association with the other cave animals. In comparing the two specimens, certain differences in the size and proportions of the dentition are evident, but whether these are individual or taxonomic has not been established. The teeth of no. B405 are imperfect and measurements difficult to obtain, but the specimen probably is to be referred to *Bassariscus astutus*.

Felis concolor? True

A number of skeletal elements of the puma or cougar have been obtained, perhaps pertaining to a single, young individual. Included are: the palatal-facial part of a skull with complete dentition, no. B272; a right ramus with damaged but complete dentition except for canine, no. B239; a number of

vertebrae, foot elements, and miscellaneous parts of the appendicular skeleton. Depths ranged from about 2 feet 6 inches to 3 feet 6 inches.

Apparently this large cat is a true puma, as is shown by several features in the dentition. The teeth are relatively heavy and thick transversely, but this character is probably due to the youth of the animal. *Felis concolor* has a very extensive range throughout parts of two continents. It occurs today on both sides of the Grand Canyon. With the present material, an attempt to identify the subspecies associated with the Rampart Cave fauna is not justified.

Lynx species

The distal end of a tibia, no. B222, demonstrates the presence of *Lynx* in the cave fauna. It was obtained from pit B at a depth of 3 feet. The specimen is not sufficient for more than a generic determination. *Lynx rufa baileyi* is common on both sides of the Grand Canyon, and in the surrounding desert and plateau regions.

Oreamnos harringtoni Stock

(Plate 4, figures 1-3)

Oreamnos harringtoni, an extinct species of mountain goat, was described originally by Stock (1936) on the basis of fossils from Smith Creek Cave, Nevada. Specimens of this species, representing several individuals, are now known from Rampart Cave. The present record augments considerably the material representing *O. harringtoni*. Most of it occurred at depths of from 3 to 5 feet, but several specimens were from nearer the surface. Skeletal elements are so common in the small test pit B that many of these animals must have inhabited the area at the time the cave was occupied. Moreover, numerous additional specimens undoubtedly will be obtained when excavation of the cave is continued, and these should provide an answer to most of the questions raised by the present material.

As described by Stock, *Oreamnos harringtoni* differs from *O. americanus* in smaller size ("approximately two-thirds of the size (linear) of *Oreamnos americanus*"); in less erect, longer, and more curved horn cores; and in several details of the front and back cannon bones. Among the specimens from Rampart Cave are two poorly preserved horn cores, nos. B321 and B332, and five horn sheaths, nos. B97, B278, B348, B367, and B385, in several degrees of completeness. Structures such as horns in general vary markedly, both sexually and individually. Unfortunately, comparative skulls of Recent *Oreamnos* at hand comprise only four individuals: male and female skulls from Alberta, Canada, a male skull (with associated skeleton) from Cook Inlet, Alaska, and a female skull from the Copper River district of Alaska. With this relatively

limited material, the following statement of comparative characters must be regarded as tentative.

The two largest horn sheaths of *Oreamnos harringtoni*, nos. B348 (pl. 4, fig. 2) and B385, are about equal in size to those of the female skulls of Recent *Oreamnos*; the others are distinctly smaller. All are smaller than those of the male skulls. The Recent females have horns that are rather straight and compressed transversely, with a more or less distinct break in curvature at the tips. In comparison, the Rampart Cave horns have slightly greater and more continuous curvature, and in no. B348, at least, are less compressed transversely. Horn core no. B332 also has a nearly equidimensional base, but in this respect it differs from those of *O. harringtoni* from Smith Creek Cave. The horns of one of the Recent male skulls are more nearly comparable in shape with those of *O. harringtoni* than are the female ones. The other, however, is less curved, although lacking the break at the extreme tips, and more compressed in the median part. The shape of the sheaths from Rampart Cave apparently reflects the characters of the horn cores given by Stock, and it may be postulated that in general the horns of *O. harringtoni* are more inclined and have greater backward curvature than those of *O. americanus*.

The dentition of *Oreamnos harringtoni* is represented at Rampart Cave by two maxillary fragments: no. B280 with DP⁴-M¹, and no. B307 with DP⁴-M². These teeth are nearly comparable in size and other characters with those in the female skulls of the living form.

The larger sheaths, possibly representing males, and the cheek teeth of *O. harringtoni* apparently are close in size to these elements in females of Recent *Oreamnos*. The forefoot of the fossil species is distinctly smaller than that of a female of the living form available for comparison. Hence, the question of a relative difference in head size might be raised, but it seems more probable that any disparity is due to the fact that the fossil specimens are compared with a few Recent specimens representing different races and presumably somewhat different size groups.

The anterior appendicular skeleton is known principally by an incomplete left leg including radius, ulna, magnum, scaphoid, lunar, metapodials, and phalanges, nos. B319, B328, B192, and B349 (probably all of one individual); and a smaller left forefoot complete from carpals to ungual phalanges except for one ungual phalanx, no. B294. In addition, a left scapula, no. B284; fragments of two humeri, nos. B219 and B221; and the distal end of a left radius, no. B247, are present.

The larger of the two Rampart Cave cannon bones, no. B349 (pl. 4, figs. 1, 1a), agrees closely in size with the comparable elements from Smith Creek Cave. The knob on the anterior end of metacarpal III, described by Stock, is less prominently developed in no. B349, this metacarpal being in this regard more or less intermediate between Recent metapodials and those from Smith Creek Cave. Splints representing the remnants of metacarpals II and V are

present on the Rampart Cave cannon bone. Metacarpal II is a short piece of bone lying at about the middle of the shaft. Metacarpal V extends from a short distance below the proximal articular surface to the middle of metacarpal IV. Splints are absent from the smaller of the two cannon bones, no. B294, as they are from those from Smith Creek Cave. These splints are probably rather easily lost both from fossil specimens and from Recent osteological material during the course of preparation. A front cannon bone of *Oreamnos*, U. S. Nat. Mus. no. 174617, was dissected especially for the purpose of determining the extent of the splints. In this specimen, metacarpal V is reduced to a small remnant at the proximal end of metacarpal IV. There is no trace of II. The splints representing metacarpals II and V may be rather variable in both Recent *Oreamnos* and *O. harringtoni*. Whether or not there is any significant difference in development between the two cannot be established with the present material.

The magnum, scaphoid, and lunar of *Oreamnos harringtoni* exhibit a number of minor differences, in addition to smaller size, from these elements in the Recent specimens at hand. It seems possible, however, that with larger suites of specimens the differences would disappear. Most of them are in the shape and extent of the various articular surfaces. One character in the Rampart Cave species which may prove to be of taxonomic value is the more sharply concave-convex lunar facet of the magnum.

Radius-ulna no. B319 from Rampart Cave differs in several particulars from that of M.V.Z. no. 4344, a Recent individual in the vertebrate zoology collections of the University of California. Aside from smaller size, it is distinguished by the following characters: (1) the distal part of the ulnar shaft is more reduced; (2) there is no prominent foramen in the ulna just external to the sigmoid notch; (3) the depression in the radius occupied by the inner ridge of the lateral condyle of the humerus is relatively narrow and deep; and (4) the articular surface of the distal part of the sigmoid notch is less extensive, and is divided into two parts with an interosseous space. Of the enumerated differences, (1) is possibly of real importance. The others are perhaps largely the result of individual or age variation.

Additional skeletal parts include several poorly preserved femora, a left tibia and the proximal end of a right tibia, an astragalus, an incomplete calcaneum, and several vertebrae. Again, distinctions appear on comparison with Recent material, but the importance of these cannot be evaluated at present.

It is possible that when further material becomes available the totality of minor characters distinguishing *Oreamnos harringtoni* may prove to be rather large. Hence, one may wonder whether *O. harringtoni* is really congeneric with the Recent species. At present, however, there is no valid reason for believing it distinct, and it seems a rather dubious supposition that additional collecting will demonstrate the distinct generic nature of *O. harringtoni*.

Whatever the magnitude of the characters separating the fossil species from the living, apparently the natural habitat of *O. harringtoni* was not markedly different from that of *O. americanus*. In addition to the faunal association at Smith Creek Cave already touched upon, a second perhaps should be mentioned. The California Institute of Technology has obtained recently a mammalian fauna from San Josecito Cave in the mountains of the state of Nuevo León, Mexico. Included in the fauna are the cannon bones of a relatively young individual of *Oreamnos* which are near *O. harringtoni*. Associated with this form are lemming mice (*Synaptomys*) and an extinct musk ox (*Euceratherium*), both presumably indicative of a relatively cool climate.

Ovis species

(Plate 4, figure 4)

The most characteristic and important specimen relating to the mountain sheep is a horn sheath, no. B400, found at a depth of 5 feet. This sheath is curiously fretted, apparently by the action of destructive solutions of some kind (pl. 4, fig. 4). This damage is not the work of rodents, although perhaps in part that of *Dermestes*. A left maxillary with P^2-M^2 , no. B322, and a symphyseal fragment of the mandible with incisors and canines, no. B226, are probably also to be referred to *Ovis*. The distal end of a cannon bone, no. Z14, and an incomplete thoracic vertebra, no. Z15, were found on the surface of the cave deposit, and may represent Recent sheep material. The specimens are insufficient for more than a generic determination, but the designation *O. canadensis* might be made, to indicate the presence of mountain sheep. The desert mountain sheep, *Ovis canadensis nelsoni*, lives in the region of Rampart Cave today, and once was common in the Grand Canyon area.

Equus species

Equine remains are limited to two specimens. The first is a milk incisor found at or near the surface of the cave deposit. The second, no. B355, consists of part of an ungual phalanx. Found at a depth of nearly 5 feet, it establishes the presence of extinct native horses in the fauna.

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CONTRIBUTIONS TO PALEONTOLOGY

VII

A REVIEW OF THE AMERICAN FOSSIL STORKS

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With one plate and two text figures

[Issued January 19, 1942]

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A REVIEW OF THE AMERICAN FOSSIL STORKS

INTRODUCTION AND ACKNOWLEDGMENTS

The first occurrence of a fossil stork in America was recorded from the Pleistocene of Brazil in 1869 (Moreno) and described as a new genus and species, *Paleociconia australis*. Since that time, three other American storks¹ have been recorded, all from Pleistocene deposits in North America:

Ciconia maltha Miller (1910)

Jabiru mycteria Lichtenstein (Miller, 1910; Wetmore, 1928, 1931)

Jabiru weillsi Sellards (1916)

At the time when Miller described *Ciconia maltha* from Rancho La Brea, California (1910, pp. 440-445, figs. 1-7), he also recorded *Jabiru mycteria* from the same locality (op. cit., p. 443). Later *Jabiru* was recorded from the McKittrick asphalt deposits (Miller, 1925a, p. 317), and in 1931 (Miller, p. 366) *Ciconia maltha* was listed from similar deposits at Carpinteria, California. In 1932, however, with more recent comparative material available, Miller re-assigned all California specimens originally referred to *Jabiru* to the extinct species *C. maltha*.

In the meantime, fossil stork bones had come to light in eastern North America, the first specimens being described as a new species, *Jabiru weillsi*, from Florida (Sellards, 1916, pp. 146-147, pl. 26, figs. 1-4). In 1928, Wetmore (pp. 2-3) recorded large stork bones from a cave in Cuba which he assigned to the living *Jabiru mycteria*, and in 1931 (Wetmore, pp. 17-18) he concluded that the bones from Florida, including Sellards' type of *weillsi*, were all of this living species also.

Feeling, however, that the eastern and western records were not altogether compatible, and that more material of recent *Jabiru mycteria* was necessary in order properly to understand the situation, Dr. Wetmore endeavored to secure skeletons of *Jabiru* from its native locality. Now, after several years, he has been able to obtain the desired specimens from Brazil. These, together with his eastern fossil material and a cast of Sellards' type, he has generously made available to the present writer for detailed comparison with the wealth of fossil material from the asphalt deposits of California.

Mr. Herman Gunter, of the Florida State Geological Survey, has also kindly lent material from the Survey's collections, and the Cuban bones have been sent on from the American Museum of Natural History through the courtesy of Mrs. Rachel Nichols. The localities east of California include: American Falls, Idaho (U. S. National Museum specimen not heretofore recorded); Ciego Montero, Cuba; and the following sites in Florida: Seminole Field, Melbourne,

¹This study concerns only the true, ciconine storks and does not include the Mycteriinae.

Vero, Itchtucknee River, and Bon Terra Farm 29 miles south of St. Augustine (E. B. Howard in Carnegie Inst. Wash. Year Book No. 39, pp. 309-312, 1940). The material from these sites consists of the following specimens:

Coracoid: four incomplete, Florida
 Scapula: two incomplete, Florida
 Humerus: cast of type specimen of *Jabiru weillsi*, Florida
 Ulna: one distal end, Florida
 Carpometacarpus: three nearly complete and three incomplete, Florida
 Tibiotarsus: three distal ends, Florida; one distal end, Idaho; one distal end, Cuba
 Tarsometatarsus: one proximal, two distal ends, Florida; one distal end, Cuba

In California, more than three hundred specimens are available from Rancho La Brea, representing all the principal skeletal elements. These are largely in the Los Angeles Museum collections. A few measurements have been made on specimens from the Museum of Paleontology, University of California, and an upper mandible (cotype of *Ciconia maltha*) was kindly loaned by R. A. Stirton of that museum. A small representation from the McKittrick asphalt deposits in the collections of the California Institute of Technology was loaned through the courtesy of Dr. Chester Stock. The McKittrick material includes two nearly complete lower mandibles and a good part of an upper mandible, as well as several mandibular fragments. These and the smaller upper fragment from the University of California collection of Rancho La Brea material, and three fragments of lower mandible from the Los Angeles Museum, represent the only available specimens of the beak of the fossil stork. Skeletal elements of *Ciconia maltha* from the Carpinteria asphalt deposits in the collections of the California Institute of Technology were also examined. Since the latter were, however, in all cases duplicates of the material from Rancho La Brea and McKittrick, they have been given no separate consideration here.

With all the North American fossil stork material at hand, it is regrettable that some statement cannot be made at this time regarding the relationships of the South American *Paleociconia australis* as well. Owing to present circumstances, however, the two known specimens of *Paleociconia*, along with other types and valuable specimens in the collections of the British Museum of Natural History, have been removed and stored in safer quarters. They were thus not available for study when Henry Anson Wylde, of the Department of Paleontology, Los Angeles Museum, visited the British Museum late in 1939. To judge from the illustration given by Lydekker (1891, fig. 15, p. 64), the South American tarsometatarsus does not resemble the North American bones. The old line drawings, however, are not always to be relied on for accuracy.

Recent comparative material available for this study includes the following specimens from the collections of the U. S. National Museum, Dr. Loye Miller, and the Los Angeles Museum: *Jabiru mycteria*, seven complete skeletons; *Ciconia ciconia*, three complete, one body skeleton; *Euxenura galatea*.

two complete, two incomplete skeletons; and *Leptoptilos crumeniferus*, two complete skeletons. The latter species differs so markedly from the fossil material, however, that it is not included in the detailed discussion.

Many of the fossil elements, particularly those from California, were previously described at some length and compared with a limited number of Recent specimens. The purpose of the present report, therefore, is not so much to furnish a detailed description of the fossil bones as to select the outstanding characters which relate to or separate them from living species. The California fossils, being most abundantly represented, form the fundamental basis for comparison. The diagnostic characters are then checked in the eastern fossil material.

Throughout this study Dr. Loye Miller has been an ever ready consultant, and I wish to extend grateful acknowledgment to him for many suggestions and for his checking of the final results.

The illustrations have been prepared by David P. Willoughby.

I am indebted to Dr. Chester Stock for criticism of the manuscript.

GENERAL DISCUSSION

From a comparative study of the fossil and recent stork material now at hand, it is evident that (1) even disregarding size, *Jabiru* stands apart from *Ciconia* and *Euxenura*, the latter two resembling each other more closely than either resembles *Jabiru*; (2) the fossil specimens from Rancho La Brea, McKittrick, and Carpinteria, California are distinct from *Jabiru* in all essential characters, falling rather into the *Ciconia-Euxenura* type; (3) the eastern Pleistocene stork bones likewise are of the *Ciconia-Euxenura* type as contrasted with *Jabiru*, and, except for a tendency to greater size, agree in all respects with the western fossils.

Regarding the generic relationship of the species from the asphalt, it is found that of the forty-odd characters analyzed, *maltha* agrees with both *Ciconia* and *Euxenura* in twenty, is distinct from both in eight, is closest to *Euxenura* in two, and is closest to *Ciconia* in fourteen. It is, of course, possible that the fossil represents a genus distinct from both *Ciconia* and *Euxenura*, but as the number of instances in which it is aligned with *Ciconia* overbalances the number in which it is distinct, it appears inadvisable to erect a new genus for the Pleistocene bird. This study, therefore, supports Miller's original decision in allocating the extinct species.

Since the eastern specimens resemble the western bones in all essentials, they are also assigned to *Ciconia maltha*. It is suggested, however, that in view of a slight tendency to larger size, the Florida bird may merit subspecific separation, in which case Sellards' name *weilli* is the appropriate designation.

Ciconia maltha can be classed as one of the giant storks, comparing favorably in tarsal length (250 to 320 mm.) with *Xenorhynchus asiaticus* (278 to

304 mm.²), *Leptoptilos crumeniferus* (262 to 282 mm.), and *Jabiru mycteria* (290 to 342 mm.), and being close to *Leptoptilos dubius* (329.5 mm.), but not attaining the size of *Ephippiorhynchus senegalensis* (380 mm.). At its lowest extreme *C. maltha* overlaps *Euxenura galatea* (229 to 268 mm.) and *Ciconia boyciana* (278.5 mm.). Length of culmen can be given only in the roughest estimate on the basis of a single upper mandible and two fairly complete lower jaws. The upper segment measures 278 mm., but it is impossible to know how this length would compare with culmen length measured externally on the skin. One of the lower mandibles indicates a still longer beak as a maximum for *C. maltha*. The mandibles are long, slender, and comparatively straight, indicating a bird with a beak much less ponderous than that of *Leptoptilos*, *Ephippiorhynchus*, or *Jabiru*, and considerably straighter than that of either of the latter two.

In proportions, *C. maltha* was apparently similar to *C. ciconia* except for relatively longer beak. Compared with *Euxenura* and *Jabiru* it was longer of wing, and in all respects it was a more slender form than the latter.

A recently mounted skeleton of *Ciconia maltha* (see plate 1), assembled from bones in the Rancho La Brea collections of the Los Angeles Museum, reveals the slender proportions of the Pleistocene bird combined with great height. The skeletal elements chosen for this composite mount are all slightly above the average length for the species. The long beak, modeled from specimens in the California Institute of Technology collections from McKittrick, is believed to approximate closely the true length of the beak in relation to the skeleton as a whole.

The mount stands 48½ inches from its base to the top of the cranium, a height exceeding that of *Ciconia ciconia*, *Euxenura galatea*, and some individuals of *Jabiru mycteria* as estimated from living birds at the San Diego Zoological Park.³ Undoubtedly, however, *Jabirus* do attain a height of as much as 5 feet (Hudson, 1920, p. 117), though in life they may appear shorter, since the neck is normally less extended than in the more slender Maguari and European storks, to which the fossil is most closely related.

DETAILED DESCRIPTION

Cranium

The cranial characters of *Ciconia maltha* as compared with *Euxenura galatea* and *Ciconia ciconia* were described at some length by Miller (1938). *Jabiru*, however, was not considered at that time. It should be pointed out, therefore, that in the present study *Jabiru* is seen to deviate widely in all respects except one (see item 6 below). In brief, the outstanding characters of the fossil are: (1) Brain case highest point in profile of skull and clearly marked

²Measurements of living species not represented by skeletons taken from Sharpe (1898, pp. 291-320).

³Thanks are gratefully extended to Mrs. Belle Benchley, Director of the San Diego Zoological Park, for the privilege of studying the storks in the Park.

off from bordering supraorbital ridges as in *Euxenura galatea* and *Ciconia ciconia*; dorsal surface of cranium of *Jabiru* broadly rounded from one supra-orbital ridge to the other, with no distinct demarcation of the brain case. (2) Nasofrontal area depressed centrally, raised slightly at edges; this character approximated in *Ciconia*, less so in *Euxenura*, and not at all in *Jabiru*. (3) Narrowing in region of parietal fossa more marked than in *Jabiru* and resembling *Ciconia*; *Euxenura* between *Ciconia* and *Jabiru*. (4) Occiput narrower than in *Jabiru* and close to *Euxenura* and *Ciconia*. Ratio of breadth of occiput to breadth of cranium: fossil, 75-78 per cent; *Jabiru*, 85-91 per cent; *Euxenura*, 77-79 per cent; *Ciconia*, 75-78 per cent. (5) Distinct ridge bordering occiput inferiorly, and definitely demarcating it from the anteriorly situated exoccipitals; faint line and irregular foramina marking the area in *Euxenura* and *Ciconia*; *Jabiru* smoothly and broadly rounded and foramina inconspicuous. A pair of foramina are present on the ridge in the fossil. (6) Proportion of height to breadth of cranium closest to *Ciconia*. Ratio in fossil, 67.5-71.7 per cent; *Jabiru*, overlapping with 70.8-74.8 per cent; *Euxenura*, relatively higher, 78.4-81.1 per cent; *Ciconia*, 70.5-72.9 per cent.

Measurements: Fossil, breadth of cranium 54.9-58.8 mm., height of cranium 38.4-41.0 mm.; *Jabiru*, breadth 59.2-66.0 mm., height 43.5-49.2 mm.; *Euxenura*, breadth 48.4-51.3 mm., height 38.6-41.2 mm.; *Ciconia*, breadth 47.1-49.1, height 34.3-34.6 mm.

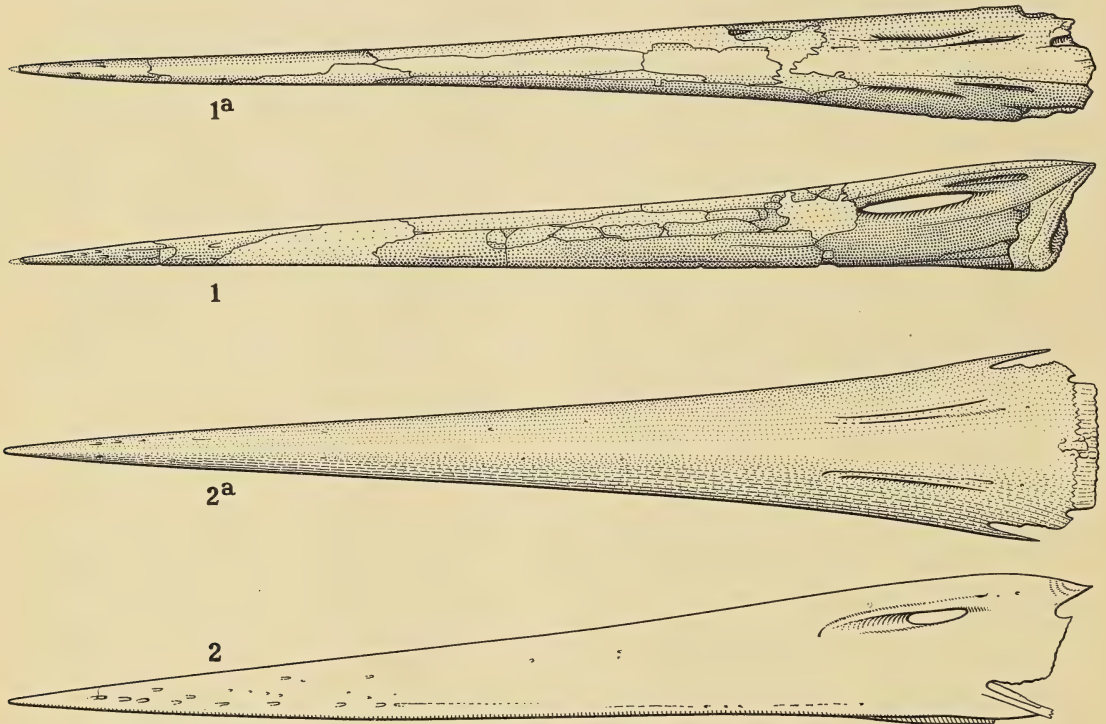
Upper Mandible

To the narial fragment of the upper mandible, cotype of the species *Ciconia maltha*, there have now been added a fairly complete rostrum and two tip fragments from the McKittrick deposits. The nearly complete mandible, with cranium (Calif. Inst. Tech. no. 1894), was considered briefly in a former discussion of the cranium (Miller, 1938). Since then, however, it has been restored so that description and illustration are possible (see fig. 1). It is restored in three pieces, two of which have a clear point of contact, though the tip third is admittedly questionable. From a study of the general slope of the upper part of the beak and of other available tip fragments, however, it is believed that the present restoration represents essentially the correct shape and size of the element. It is evident that the fossil rostrum in no wise resembles the deep, upward-curving beak of *Jabiru mycteria* (see figs. 1, 2). The difference is further emphasized by the lower mandible, two fairly complete specimens of which are now available, as well as several fragments. All mandibular material is of the slender type with nearly straight rami, characteristic of *Ciconia ciconia* and *Euxenura galatea* as distinguished from *Jabiru mycteria*.

When the cotype rostral fragment was described (Miller, 1910, p. 444, figs. 6, 7), it was stated that "the most liberal restoration indicates a maximum length of 210 mm." This calculation was exceedingly modest, as can now be

observed from the additional material. The McKittrick specimen, which in breadth and height is slightly smaller than the cotype, measures 278 mm. over all, or 243 mm. to the posterior edge of the narial opening, a length slightly exceeding that of the smallest of the available specimens of *Jabiru* and considerably greater than that given for the culmen of *C. boyciana*, the largest living representative of the genus *Ciconia*, 9.5 inches or 240.2 mm. (Sharpe, 1898, p. 303).

Detailed characters of the fossil beak are: (1) posterior end of culmen lacking dorsal "hump" characteristic of *Euxenura*, being broadly and gradually



Figs. 1, 1a. Upper mandible of *Ciconia maltha* from McKittrick Pleistocene, California. C.I.T. no. 1894. Fig. 1, lateral view; fig. 1a, dorsal view. $\times 0.5$.

Figs. 2, 2a. Upper mandible of Recent *Jabiru mycteria* from Brazil. U. S. Nat. Mus. no. 343465. Fig. 2, lateral view; fig. 2a, dorsal view. $\times 0.5$.

rounded as in *Ciconia*; (2) upper edge of external nares straighter than in the other forms compared; particularly distinguished from *C. ciconia*, in which this edge is jagged; (3) ventrally, narrow groove separating maxillaries from maxillopalatines deep cut and extending anteriorly well beyond the external nares; in this respect the resemblance is closest to *Ciconia* and least close to *Jabiru*; the ventral extent of the palatal side of the groove below the maxillary, however, is more suggestive of *Euxenura*.

Relative to length (taken from posterior edge of nares to tip of beak), the height and breadth of the McKittrick fossil mandible are less than in any of the compared forms: fossil ratios (height and breadth measured at anterior

edge of nares), height 9.4, breadth 9.2 per cent; *Jabiru mycteria*, 14 and 13 per cent respectively; *Euxenura galatea*, 11.3 and 11.1 per cent respectively; *Ciconia ciconia*, 14 and 10 per cent respectively. The measurements of breadth and height are nearly equal in the McKittrick fossil, as is true also of *Euxenura*, but the beak of *C. ciconia* is considerably broader than high. The Rancho La Brea cotype shows slightly greater relative breadth, but is still not so broad relatively as *Ciconia*. All measurements on the fossil mandible, however, are approximate, as the fragility of this element admits the possibility of warping and displacement.

Lower Mandible

As previously described by Miller (1932, pp. 215-216) the lower mandible of *Ciconia maltha* is a longer, more slender element than that of *Jabiru*, though with a shorter symphysis, agreeing closely in this proportion, though not in actual size, with *C. ciconia*. Six additional fragments from Rancho La Brea and McKittrick and another practically complete specimen from the latter locality emphasize the slenderness of the fossil jaw. All the additional symphyseal material agrees with the previously described specimen (Calif. Inst. Tech. no. 138/293) in the very slight upward curvature toward the tip, and one specimen is even as straight as in *C. ciconia*.

Since the measurements of no. 138/293 were recorded, a correction has been made in the restoration of the specimen, so that the greatest depth of the ramus now measures 25.3 mm. instead of 25.7, the total length 350 mm. instead of 355, and the length of symphysis 105.5 mm. instead of 106.5. The ratio of symphyseal length to total length of ramus (30 per cent), however, remains the same. It is probable that this specimen is of nearly maximum size for *C. maltha*. The other nearly complete jaw has an over-all length of approximately 321 mm. and a symphyseal length of 108.5 mm., giving an approximate ratio of 33.8 per cent; greatest depth of ramus 23.7 mm. The two separate symphyses measure 94.1 mm. and 105 mm. respectively. Measurements of living species are: *Jabiru mycteria*, total length 315-342 mm., symphyseal length 147-169 mm., ratio of symphysis to total length 45-50 per cent, depth of ramus 30-33 mm.; *Euxenura galatea*, total length 248-287 mm., symphysis 93-109 mm., ratio 38 per cent, depth of ramus 19-21 mm.; *Ciconia ciconia*, total length 207-216 mm., symphysis 55.3-67 mm., ratio 26.7-31 per cent, depth of ramus 15.5-16.8 mm.

Sternum

The fossil specimens of this element are very fragmentary and come only from the California localities. Certain characters are determinable, as follows: (1) Point of greatest depth of keel nearer anterior end than in *Jabiru*; similar to *Euxenura* and *Ciconia* though with less acute upward curvature of keel anteriorly beyond manubrium than in the former. (2) On dorsal side, one central pneumatic opening posterior to manubrium as in *Euxenura* and

Ciconia, though closer to the latter in having a single perforation farther posterior to the manubrium and the entire dorsal area less excavated; *Jabiru* with two shallow lateral openings just posterior to the manubrium, and behind these a deeply grooved central area perforated with a line of small openings. (3) Nearly half of anterior carinal margin deeply excavated as *Ciconia*; *Euxenura* excavated for a lesser distance; *Jabiru* very variable in this character, so it is possible that the character is unreliable.

Size. Exact measurements are impossible on the fossil material. Estimated average length 128 mm., with depth of keel 71 mm., agreeing closely with the size of *Jabiru*, though the latter appears proportionately deeper of keel. *Euxenura galatea*, average length 109 mm., depth of keel 63 mm.; *C. ciconia* considerably smaller (95 mm. and 55 mm.).

Furcula

Incomplete material, from Rancho La Brea only, shows the following characters: (1) Facet of furcular process for attachment to sternal carina broadly rounded and faintly depressed; generally similar to *Euxenura* and *Ciconia*; facet long, oval, narrow, and deeply concave in *Jabiru*. (2) Coracoid attachment lacking the depth of excavation found in *Jabiru*; area more smoothly rounded throughout as in *Euxenura* and *Ciconia*, though with dorsal contour more concave.

Scapula

The fossil scapula closely approximates *Jabiru* in breadth of head, averaging 24.9 mm. in the California bird, 25.1 mm. in *Jabiru*. This area seems somewhat constricted in the latter form, the acromion and glenoid appearing to be bent together dorsally to form a narrow, deep concavity between, while ventrally the shaft is convex. The dorsal area in the fossil is broader and more shallow, the ventral side more flattened. *Euxenura* and *Ciconia* are similar to the fossil in general contour of the area, but a depression present under the coracoid articulation in the fossil is less marked in *Ciconia*, and absent in *Euxenura*.

The two scapulae from Florida, possibly right and left of one individual, are similar to the western specimens, though they exceed by 0.6 mm. the largest of the latter (maximum breadth of head in ten western specimens, 26.4 mm., Florida measurement 27.0 mm.).

Coracoid

The character of the head of the coracoid is distinctive in each of the forms compared. In all fossil bones from California the dorsal contour is slightly and evenly rounded from front to back, with the surface above flattened from left to right and extending almost to the anteriormost tip of the furcular facet. The dorsal contour in *Euxenura galatea* and *Ciconia ciconia* appears less rounded and less even, owing to the discontinuance of the dorsal

surface considerably above the anterior tip of the furcular facet; the contour is further at variance with that of the fossil in *Euxenura*, in which the flattened dorsal surface rises to a high point posterior to the mid-point and slopes rather sharply anteriorly; in *Ciconia* the dorsal surface is slightly undulating rather than flat. *Jabiru* is distinctly different from the others in the markedly convex dorsal contour, with dorsal surface sloping off to the outside, forming an uneven, convex area.

Other characters of the fossil which are similar to those of *Ciconia* and *Euxenura* but distinct from those of *Jabiru* are as follows: (1) brachial tuberosity extending farther internally than in *Jabiru*; (2) sternocoracoidal impression markedly depressed; practically no depression in *Jabiru*; (3) breadth of furcular facet 8 to 14 per cent greater than breadth of bone below this facet; in *Jabiru*, furcular facet 18 to 24 per cent broader than body of bone below.

Owing to the condition of the four dorsal ends of coracoid from Florida, all the above characters cannot be checked in detail except in one specimen, which agrees with *Ciconia maltha* throughout. The resemblance to *maltha* in extent of brachial tuberosity is evident in all, and in two specimens the head, though broken, is clearly of the *Ciconia-Euxenura* type as in *C. maltha*. These two bones are slightly larger than the California bones, with a breadth of furcular facet of over 26 mm. The largest of the California specimens measures 25.9 mm. at this point.

In length of coracoid, seven out of seventeen specimens of *maltha* overlap *Jabiru*, and two of the smaller bones are within the size range of *Euxenura galatea*. Measurements: *maltha*, length 82.4-101.2 mm., breadth of furcular facet 21.0-25.9 mm. (Florida specimens 23.3-26.5 mm.); *Jabiru*, length 94.1-105 mm., breadth of facet 24.7-30.3 mm.; *Euxenura*, length 79.9-87.6 mm., breadth of facet, 19.0-21.3 mm.; *Ciconia*, length 69.4-76.6 mm., breadth of facet 17.9-21.0 mm.

Humerus

The papilla at the proximal end of the intermuscular lines on the anconal face of the humerus is situated at a slight angle to these lines in the fossil, but is not transversely placed as in *Jabiru*. An almost imperceptible muscle scar is present proximal to this papilla, near the median crest in the fossil and in *Ciconia*; this scar is more prominent in *Euxenura* and *Jabiru*, and in the latter is farther removed from the median crest, with the shaft slightly raised at this point.

Distally the ectepicondylar process is more projecting and higher relative to breadth of distal end in *maltha* than in *Jabiru*; *Euxenura* and *Ciconia* are similar to *maltha*. The ligamentary attachment of the entepicondylar prominence is more vertical in position in the fossil than in *Jabiru*, and there is more surface facing toward the ulnar side; *Ciconia ciconia* is closest to *maltha* in this respect.

The external surface of the deltoid crest is heavily bordered in the fossil but depressed near the shaft. In *Jabiru* the surface of the crest is flat and rounds smoothly from the shaft to its edge without intervening depression. In *Euxenura* and *Ciconia* there is a faint depression as the crest leaves the shaft, but in neither does it equal the depression in the fossil; the border is slightly enlarged in *Ciconia*.

Euxenura is distinctly set apart from the fossil specimens as well as the living by its short, prominently extended bicipital crest.

The Florida specimen (type of *Jabiru weillsi* Sellards), judged from the illustration by Sellards (1916, pl. 26, fig. 1) and from the cast, is in general agreement with the western fossils in the position of the muscle scars, the depressed deltoid crest, the high ectepicondylar process, and the position of the ligamental attachment of the entepicondylar prominence. The cast differs from the California specimens in greater distal extent of the pneumatic foramen, which may, however, be due to a break in the original bone not evident as such in the cast. At all events there is nothing to indicate that *Jabiru weillsi* Sellards should be generically or specifically separated from *Ciconia maltha* Miller.

In the western fossils the size range, based on very fragmentary material, is as follows: length 250-280 mm. approximately (original length⁴ of Florida bone as given by Sellards, p. 146, 280 mm.), breadth of proximal end 48.2-53.3 mm. (Florida cast measures 54.7 mm.), breadth of distal end 38.7-40.7 mm. (Florida cast measures 43.3 mm.); *Jabiru mycteria*, length 252.8-276.3 mm., proximal breadth 49.5-54.8 mm., distal breadth 40.4-45.7 mm.; *Euxenura galatea*, length 212.2-225.4 mm., proximal breadth 41.4-44.7 mm., distal breadth 31.8-34.9 mm.; *Ciconia ciconia*, length 195-216.2 mm., proximal breadth 37.6-40.3 mm., distal breadth 28.8-31.3 mm.

Ulna

Fossil specimens of ulna are badly worn and are incomplete. The following points of distinction from *Jabiru* can be noted, however: (1) Brachial area smooth and devoid of foramina. (2) Proximal radial depression shallow. In *Jabiru* the brachial area is more excavated and roughened and one or many foramina are present; the proximal radial depression is deep and well perforated with foramina. (3) Carpal tuberosity of distal end sharply protruding and the ligamental surface on its under side roughened and tilted slightly toward the trochlear surface; in *Jabiru* the tuberosity more rounded in contour and bending downward slightly at tip, the ligamental attachment smooth and facing downward. (4) Tendinal groove longer and more deeply cut. *Euxenura* and *Ciconia* are close to the fossil in the characters of the proximal end; distally the closest resemblance of the fossil is to *Ciconia*.

⁴Wetmore (1931, p. 17) records that since the original description of *J. weillsi* the type specimen has been broken and in process of restoration lengthened to 293 mm. owing to separation of broken parts.

The one distal end of ulna from Florida agrees with *C. maltha*. An exact measurement of length can be made on only one fossil ulna (318 mm.). It is possible, however, to derive an approximate measurement on another nearly complete specimen (338 mm.). Judging from the breadth of the ends, compared with other incomplete specimens, this latter bone is longer than the average for the fossil. The range in size in *Jabiru* is 318-357 mm., in *Euxenura* 243-264 mm., and in *Ciconia ciconia* 231-248 mm.

Carpometacarpus

In this element of the fossil, metacarpal I is short and is placed high on the shaft, differing from all living storks with which it was compared. Height of metacarpal I relative to depth of proximal end: California fossils, 51.7-55.7 per cent; Florida fossils, 51.3-54.3 per cent; *Jabiru mycteria* 56.2-61.8 per cent; *Euxenura galatea* 58.8-59.9 per cent; *Ciconia ciconia* 59.5-60.5 per cent.

In other characters the fossil is similar to both *Euxenura* and *Ciconia* as contrasted with *Jabiru*, as follows: (1) External surface of head depressed between external ligamental attachment and posterior raised edge of trochlea; this face in *Jabiru* puffy and blending into edge of trochlea without definite depressed area except for pitlike indentation immediately adjacent to ligamental attachment. (2) Internal surface of proximal symphysis nearly straight across at base of trochlea and metacarpal I, with only a shallow depression near point of union of metacarpals II and III; *Jabiru* with depression more pronounced and accentuated by inward projection of metacarpal III, and usually by small foramina extending through the depression to base of pisiform process; further pneumaticity noted in *Jabiru*, but not in fossil, in area anterior to trochlea. (3) Posterior view, upper part of metacarpal III straight-sided; in *Jabiru* this area irregular with internal side overdeveloped at point of muscle attachment and external side slightly deviated beneath the trochlea. (4) Distally, posterior angle of metacarpal III more rounded, less acute than in *Jabiru*.

In all the above characters the two complete fossil carpometacarpi from Florida agree with *C. maltha*. The more fragmentary material agrees in all characters which pertain to areas which are not broken. All are clearly of the *Ciconia-Euxenura* type as contrasted with *Jabiru*.

The fossil carpometacarpi average slightly longer than those of *Jabiru*, though they are more slender of shaft and have a less heavy head region. There is no overlap in length with either *Ciconia ciconia* or *Euxenura galatea*, though proportionately there is a similarity to the former, *Euxenura* being relatively stouter.

Measurements: California fossils, length 129.5-150 mm., breadth of shaft at middle 9.0-10.4 mm., ratio of breadth of shaft to length 6.4-7.2 per cent; Florida fossils, length 144.5-151.5 mm., shaft 10.4-10.5 mm., ratio 6.8-7.2

per cent; *Jabiru*, length 129.3-143.3 mm., shaft 10.3-11.0 mm., ratio 7.6-8.2 per cent; *Euxenura*, length 113.0-120.8 mm., shaft 8.0-9.0 mm., ratio 7.0-7.5 per cent; *Ciconia*, length 105.5-116.3 mm., shaft 7.2-7.6 mm., ratio 6.3-7.0 per cent.

Femur

Like the femur of *Ciconia ciconia* and *Euxenura galatea*, the fossil femur is a more slender-shafted bone than that of *Jabiru mycteria*. Also the proximal end is more flared, the trochanter bulging out before its inward curve to the articular end, whereas in *Jabiru* the trochanteric area makes a long, continuous curve inward and upward. *Jabiru*, however, agrees with both the fossil and *Ciconia ciconia* in the marked extent of the trochanteric ridge above the articular surface; in *Euxenura* the ridge is shorter.

The intermuscular lines of the posterior surface in the fossil resemble those in *Ciconia* and *Euxenura* in their union midway up the shaft and continuation from this point as a single line. In *Jabiru* the two lines remain distinct well above the center of the bone.

This element is not represented in the eastern fossil specimens.

In length *C. maltha* exceeds *Jabiru* at the maximum end of its range, though it averages slightly less. It overlaps *Euxenura* with one specimen of minimum size. Measurements of length: fossil, 105.2-123.2 mm.; *Jabiru mycteria*, 112.0-121.9 mm.; *Euxenura galatea*, 101.1-109.6 mm.; *Ciconia ciconia*, 85.0-94.2 mm.

Tibiotarsus

Characters of the tibiotarsus of *C. maltha* have been given at length (Miller, 1910, p. 443; 1925^b, p. 75; 1932, p. 214) and need not be repeated at this time. Three outstanding characters should serve to distinguish the fossil from *Jabiru*, and one of these is sufficiently distinctive to separate it from *Euxenura* and *Ciconia* as well. (1) Ligamental attachment above distal external condyle a prominent ridge, broadening distally, and with pointed proximal end merging into the shaft; in *Jabiru* the attachment is a prominent papilla rather than a ridge; the ridgelike nature of the attachment is common to *Ciconia* and *Euxenura*, though in the former it lacks the prominence of the fossil ridge, and in the latter it juts out more sharply from the shaft proximally. (2) Proximal border of cnemial crest only slightly depressed as in *Euxenura* and *Ciconia*; abruptly notched in *Jabiru*. (3) Distance between internal and external cnemial crests (along proximal border) relatively greater than in *Jabiru*; ratio of this distance to breadth of cnemial region, 63.4-68.3 per cent in the fossil, 53.4-60.7 per cent in *Jabiru*, 63.6-65.0 per cent in *Euxenura*, 63.2-64.8 per cent in *Ciconia ciconia*.

The eastern bird cannot be judged on points 2 and 3, as no proximal ends of the element are available. In the character of the distal end, however, the five eastern bones agree with *C. maltha*.

There are only five fossil specimens on which exact length can be measured. These range from 315 to 363 mm.; two other nearly complete tibiotarsi have an estimated length of over 370 mm. Length in living species: *Jabiru mycteria*, 347.8-394.7 mm.; *Euxenura galatea*, 273.2-309.8 mm.; *Ciconia ciconia*, 239.2-258.9 mm. Breadth of distal end measured in twenty-five western fossil specimens, 18.0-21.5 mm.; three Florida fossils, 19.4-21.4 mm.; one Idaho fossil, 18.6 mm.; one Cuban fossil, 20.8 mm.; *Jabiru*, 18.2-22.2 mm.; *Euxenura*, 16.8-18.8 mm.; *Ciconia*, 14.3-15.6 mm.

Tarsometatarsus

Like the preceding element, the tarsometatarsus has been fully described before (Miller, op. cit.). Since, however, the characters of this element are complex and certain points of variability have been noted in the added Recent material now at hand, it seems advisable to treat it at some length again.

This element in the fossil species is similar in general characters to that in *Ciconia ciconia* and *Euxenura galatea*, though 25 to 30 per cent larger than the former and overlapping the latter with only one specimen. The size more closely approximates that of *Jabiru*, but the angularity of *C. maltha*, compared with the rounded surfaces in *Jabiru*, gives the fossil bone the appearance of greater slenderness. Distally the shaft of the fossil narrows abruptly above the trochleae, slenderizing this area as compared with both *Euxenura* and *Jabiru*. The hypotarsus, also, is more slender than in *Jabiru*; greatest breadth of hypotarsus relative to breadth of proximal articular surface: California fossils, 52-60 per cent; Florida fossil, 57.6 per cent; Cuban fossil, 57.6 per cent approximately; *Jabiru mycteria*, 62-64 per cent; *Euxenura galatea*, 55-57 per cent; *Ciconia ciconia*, 51-53 per cent.

Other diagnostic characters of *C. maltha*, contrasted with *Jabiru* and agreeing with *C. ciconia* and *Euxenura* unless otherwise indicated, are as follows:

(1) Hypotarsus noticeably set off from proximal end by straight drop down from cotylar area and deep pit between the narrow calcaneal ridges at their proximal surface; in *Jabiru*, position less distant from proximal end, with more gradual drop and no marked excavation of proximal surface of hypotarsus; *Ciconia* and *Euxenura* closer to fossil though excavation not always so marked.

(2) Calcaneal ridges more slender and more pointedly extended proximally. External ridge exceeding internal in length and 31 to 49 per cent longer than the distance across the hypotarsus; in *Jabiru*, internal ridge sometimes exceeding external, but neither ever more than 18 per cent longer than breadth of hypotarsus (average length 108 per cent of hypotarsal breadth).

(3) Intercotylar tuberosity relatively broader and more blunt at tip and more inclined toward external side; slight excavation present at external side of base of tuberosity anteriorly though much less marked than in *Jabiru*; breadth and slant of tuberosity closer to *Ciconia* and *Euxenura* but excavation at base

absent in these genera. (5) Internal distal trochlea more slender posteriorly and in this respect closer to *Ciconia* and *Euxenura*, although differing from them in more gradual downward slope from shaft to tip.

With the exception of one fragmentary distal end from Florida in which the areas referred to above are missing, the eastern bones agree in all respects with the description of *C. maltha* given above. The length of the external calcaneal ridge cannot be taken in the Cuban bone, owing to breakage, but even the internal ridge is longer than the longest in *Jabiru*.

Measurements in millimeters:

	Length	Breadth, proximal end	Breadth, distal end
California fossils259.5-320 ^b	20-24.5	23-28
Florida fossils	23.3	26.0
Cuban fossil	24.3
<i>Jabiru mycteria</i>290-342	22-25.1	25.7-29.6
<i>Euxenura galatea</i>229.4-267.8	19.4-22.3	22.3-24.7
<i>Ciconia ciconia</i>205-230.2	16.2-18.3	19.3-20.1

SUMMARY AND CONCLUSIONS

All the known North American fossil stork bones have been compared with the two living storks with which they show closest relationship, *Ciconia ciconia* and *Euxenura galatea*, and with the large American stork *Jabiru mycteria*. The fossil wood ibis has not been considered in this study.

The previous assignment of all fossil stork specimens from California to the extinct species *Ciconia maltha* is substantiated.

All eastern fossil stork bones are also assigned to *Ciconia maltha*, though it is suggested that the Florida bones, tending to slightly larger size, may represent a separate subspecies, which should bear Sellar's original designation *weillsi* as the subspecific name--*Ciconia maltha weillsi*.

With the assignment of the eastern bones to *C. maltha*, the living species, *Jabiru mycteria*, is removed from the fossil record, and the "La Brea" stork is added to *Teratornis* and the California condor as a species of wide distribution in the Pleistocene.

^bThe measurement of 256 mm. for the type tarsus (Miller, 1910, p. 445) is an actual measurement on a warped specimen. It is believed that normally the bone would have been nearly 4 mm. longer.

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Mounted skeleton of *Ciconia maltha* assembled from Rancho La Brea bones in the collections of the Los Angeles Museum. Beak modeled after specimens in the California Institute of Technology collections from McKittrick.

Mounted by Eugene J. Fischer, L. A. Museum.
Photograph by Edward S. Cobb, L. A. Museum.

CONTRIBUTIONS TO PALEONTOLOGY

VIII

THE SOUTH AFRICAN MAN-APES AND PITHECANTHROPUS

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With ten plates and six text figures

[Issued July 22, 1942]

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THE SOUTH AFRICAN MAN-APES AND PITHECANTHROPUS

INTRODUCTION

In 1925 R. A. Dart described a juvenile anthropoid skull, from a cave near Taungs in South Africa, which shows a remarkable development of the brain and a high specialization of the face and the dentition. There has been much discussion about this skull, to which Dart gave the name *Australopithecus africanus*. Dart has suggested that it is related to the hominids, as have also R. Broom (1938b), W. K. Gregory (1939b), and A. S. Romer (1930). On the other hand, we find the opinion expressed that *Australopithecus* belongs among the typical anthropoids. It has been regarded as a young gorilla by O. Abel (1928), as a species having the same ancestor as the gorilla by W. Abel (1931), as nearer to the gorilla than to the chimpanzee by W. L. H. Duckworth (Keith, Smith, Woodward, and Duckworth, 1925), and as very near to the chimpanzee by Weinert and Sir Arthur Smith Woodward. Finally, Sir Arthur Keith and G. Elliot Smith consider it a new genus of anthropoid.

New material discovered since 1936 by R. Broom (1936, 1938a, 1938b) has thrown fresh light on this interesting and, for our knowledge of the evolution of man, very important problem. Broom's finds belong to closely related but slightly different species, one of which he at first regarded as *Australopithecus* (*Australopithecus transvaalensis* Broom). Later he called his new finds from Sterkfontein *Plesianthropus transvaalensis*, and those from Kromdraai *Paranthropus robustus*.

The new material consists mainly of skull fragments with parts of the upper jaws of both species, besides the greater part of a right lower jaw of *Paranthropus* and a lower canine, a first lower premolar, and a last lower molar referred to *Plesianthropus*, all from adult specimens. The most striking fact is that the dentition, carefully studied on the actual material by W. K. Gregory and M. Hellman and on the casts by G. Montandon (1939), is of almost human appearance. There can be no doubt that the subfamily Australopithecinae Gregory and Hellman 1939 (= Paranthropinae Montandon 1940) is more closely related to the hominids than to the anthropoids. Gregory and Hellman come to the conclusion that "these South African Pleistocene man-apes were both in a structural and a genetic sense the conservative cousins of the contemporary human branch" (1939a, p. 371).

Dart (1926) wrote of *Australopithecus*: "These features . . . are of such a nature as to lead me to believe that the brain and bodily form of the South African Man-Apes had attained a stage of organization which lifts them out of the category of the living anthropoid apes and places them in a separate genus and probably in a separate family of beings intermediate between the chimpanzoid group of anthropoids and the most primitive known forms of mankind, the Pithecanthropidae."

COMPARISON BETWEEN PITHECANTHROPUS AND SOUTH AFRICAN MAN-APES

This latter problem will be discussed here in detail. During recent years more remains of *Pithecanthropus* have been discovered by the present author, with aid from the Carnegie Institution of Washington, and now comparison with the man-apes of South Africa has become possible. The new material (see illustrations) demonstrates beyond any doubt that *Pithecanthropus* is a member of the human family. This material includes the heavy mandible B, which can be directly compared with the heavy mandible of *Paranthropus*. There is also the skullcap *Pithecanthropus* II of a female individual; and the incomplete male skull IV shows the upper palate. This last skull has not been described, but some general remarks on the dentition may be given here.

Skull

The brain capacity of the Australopithecinae is less than that of *Pithecanthropus*. *Australopithecus* has a brain capacity of about 450 cc. (adult, estimated by W. Abel); *Plesianthropus* female has about 440 cc., *Paranthropus* male 600 to 650 cc., according to Broom. *Pithecanthropus* has about 835 cc. in the female and about 1000 cc. in the male. The processus mastoideus in *Pithecanthropus* II is very weak, being developed in the same degree as in the anthropoids, and differing from that in man, which is very pronounced. The glenoid fossa, flat in the anthropoids, is deep in *Pithecanthropus* as in *Homo*, and in *Paranthropus* seems to demonstrate a somewhat intermediate stage. The prognathism of *Plesianthropus* is said to be less than that of modern apes, but it is more developed than in *Pithecanthropus* IV, which, for such a primitive hominid, shows considerably less prognathism than might be expected (von Koenigswald and Weidenreich, 1939).

Mandible

The symphysis of *Paranthropus* shows about the same conditions as are observed in gorilla. The planum alveolare is well developed (as also in *Australopithecus*), and there seems to be no fossa digastrica, so far as can be judged from the fragment. In *Pithecanthropus* B there is no planum alveolare, a feature which in fossil man is observed only in the mandibles of Heidelberg and Ehringsdorf; there is a well developed digastric fossa and, as in the Heidelberg jaw, an incisura submentalis. In *Paranthropus*, furthermore, the ramus ascendens is projected more forward than in *Pithecanthropus*.

Adult Dentition

Upper dentition. It is a striking fact that the dental arch in *Plesianthropus* is very human-like, whereas *Pithecanthropus* is much more like the anthropoids in this respect. M³-C in *Pithecanthropus* are arranged in a straight line, the dental arches are slightly convergent, and there is a pronounced diastema in front of the canines. Such a diastema is absent in all other hominids as well

as in the Australopithecinae. The upper canine, unfortunately very worn in *Pithecanthropus*, cannot have been very protrudent and was of about the same size as in *Paranthropus*. *Pithecanthropus* resembles *Plesianthropus* and *Paranthropus*, and differs from recent man, in that the first upper premolar has three roots and the second upper molar is larger than the first, so that in this respect *Pithecanthropus* is nearer to the man-apes and anthropoids than it is to man.

The upper molar of *Australopithecus*, with its complicated pattern, shows certain affinities with the same tooth of *Sinanthropus*, as has been pointed out by Weidenreich (1937, p. 67). The teeth of the *Pithecanthropus* palate are very worn and do not show sufficient details for a close comparison, but they seem to be simpler.

Lower dentition. Neither the canine nor the first premolar (P_3) of *Pithecanthropus* is known. In *Paranthropus* "this crown as well as that of P_2 "--the second premolar is P_4 of our description--"is essentially like that of *Sinanthropus*" (Gregory and Hellman, 1939a, p. 351).

The heavy lower jaw of *Pithecanthropus* B, fitting perfectly into the upper jaw of the big skull IV, certainly belongs to a male individual, and the same is to be said of the heavy mandible of *Paranthropus*. In *Pithecanthropus* only the second premolar and the three molars have been preserved. The teeth are worn and not in the best condition, but show sufficient details. All teeth are very large, larger than in recent man, but smaller than in *Paranthropus* and the other Australopithecinae, as is shown in table 1.

TABLE 1

Comparative measurements (in millimeters) of lower molars and second premolars (P_4)

AP, anteroposterior diameter
Tr, transverse diameter

	P_4		M_1		M_2		M_3	
	AP	Tr	AP	Tr	AP	Tr	AP	Tr
<i>Plesianthropus transvaalensis</i>	16.6	15.0
<i>Australopithecus africanus</i>	14.2	12.8
<i>Paranthropus robustus</i>	10.5	13.3	13.6	13.3	14.5	13.6	16.2	14.0
<i>Pithecanthropus erectus</i>	9.2	11.1	12.5	13.0	13.0	13.0	14.5	12.5
<i>Sinanthropus pekinensis</i> (G)	8.5	11.0	13.2	12.5	12.5	12.7	12.0	12.3
<i>Homo neanderthalensis</i> (Le Moustier)	8.5	10.0	12.5	11.6	12.3	11.6	11.4	10.8
<i>Homo heidelbergensis</i>	7.5	9.2	11.6	11.2	12.7	12.0	12.2	10.9
<i>Homo sapiens</i> :								
Australians	7.3	8.7	11.2	11.4	10.9	10.8	11.0	10.7
White: males	7.2	8.6	11.2	10.5	10.7	10.4	10.1	10.5
females	6.8	8.2	10.7	10.2	10.0	9.8	9.9	9.5

Australopithecus after W. Abel (1931).

Premolar of *Paranthropus* after cast.

Homo neanderthalensis and *H. sapiens* after Gregory and Hellman (1926).

The dental arch in *Pithecanthropus* as well as in *Paranthropus* is slightly convex on the buccal side and shows the same conditions as in man, whereas in the anthropoids the molars and premolars are arranged in a more or less straight row.

Judging from the alveoli, the canine of *Pithecanthropus* was small and the first premolar had only one root, as has the bicuspid second molar. The length of the latter tooth, both absolutely and relatively to the length of the first molar, is small in *Homo* and *Sinanthropus* (relative values lower than 70; see table 3); it is absolutely and relatively large in *Pithecanthropus*, *Paranthropus*, and the anthropoids (relative values higher than 70). In this respect *Paranthropus* ranges among the living anthropoids, according to average measurements as given by Gregory and Hellman (1926): chimpanzee, 74.2; gorilla, 76.7; *Paranthropus*, 77.2; orang, 81.6. *Pithecanthropus* with 73.6 is intermediate between these two groups.

In the crown pattern of this tooth there is, as was mentioned above, no essential difference between *Paranthropus* and *Sinanthropus*. This tooth of *Pithecanthropus* is exactly like the same tooth of *Sinanthropus*, only less wrinkled.

In *Pithecanthropus* can be observed a remarkable and decided increase in length from the first to the third molar. This is very unexpected in a hominid, as in recent man the first molar is usually the largest and the third is irregular and often missing. Already in *Sinanthropus*, although in the heavy mandible G the second molar is larger than the first, the average of these two molars *in situ* is exactly the same (12.6 mm.), and the third molar is reduced. In recent man the average for the first molar is 11.1 mm. and for the second 10.7 mm., according to De Jonge-Cohen.

We find, however, such an increase in length also in *Paranthropus* and in the anthropoids. Here in all cases the second molar is larger than the first. Taking the first molar as 100, we find (average for the living anthropoids according to Gregory and Hellman, 1926) for orang 103.6 and for chimpanzee 104.7, both very close to *Pithecanthropus*, 104.0, and *Paranthropus*, 106.6; for gorilla 113.9, and for the fossil anthropoids 110 to 120. In the last group the third molar is always longer than the first, with values between 115 and 129. The three living anthropoids differ: in orang only is the third molar generally larger, 108.0; in chimpanzee it often has the size of the first and in gorilla of the second molar. *Paranthropus* and *Pithecanthropus* show nearly the same relative length, 119.1 and 116.0 respectively, for the third molar.

Judging by the relative lengths of the second as well as the third molars, therefore, *Paranthropus* is much nearer to *Pithecanthropus* than it is to the anthropoid apes. See table 2.

TABLE 2

Relative length of the three molars and the second premolar (P₄)(M₁ = 100)

	P ₄	M ₁	M ₂	M ₃
<i>Paranthropus robustus</i>77.2	100.0	106.6	119.1
<i>Pithecanthropus erectus</i>73.6	100.0	104.0	116.0
<i>Sinanthropus pekinensis</i> (G)64.3	100.0	94.7	90.9
<i>Homo heidelbergensis</i>64.6	100.0	109.4	105.1
<i>Homo neanderthalensis</i> (Le Moustier)68.0	100.0	98.4	91.2
<i>Homo sapiens</i> :				
Australians65.1	100.0	97.3	98.2
White: males64.2	100.0	95.5	90.1
females63.5	100.0	93.4	92.5

Homo sapiens after Gregory and Hellman (1939).

The breadth indices for the first and second molars of *Paranthropus* are lower than in *Pithecanthropus* but still within the range for man; this index for the third molar is exactly the same in *Paranthropus* and in *Pithecanthropus*. See table 3.

TABLE 3

Breadth indices of the lower molars

	M ₁	M ₂	M ₃
<i>Plesianthropus transvaalensis</i>	90.3
<i>Australopithecus africanus</i>	90.1
<i>Paranthropus robustus</i>	97.8	93.8	86.4
<i>Pithecanthropus erectus</i>	104.0	100.0	86.2
<i>Sinanthropus pekinensis</i> (G)	94.2	101.3	100.0
<i>Homo heidelbergensis</i>	96.5	94.5	89.3
<i>Homo neanderthalensis</i> (Le Moustier)	83.4	94.3	91.2
<i>Homo sapiens</i> :			
Australians	98.3-109.5	94.8-103.8	94.3-101.9
White	89.6-100.0	93.2-110.6	87.9-105.0

Homo sapiens after Gregory and Hellman (1939).

The crown shows the pentacuspoid "Dryopithecus pattern" (Gregory and Hellman) most clearly in the first molar, in *Paranthropus* as well as in *Pithecanthropus* and in recent man. But whereas in the latter the second molar is generally quadricuspoid, in *Paranthropus* and *Pithecanthropus* it is still pentacuspoid. In *Paranthropus* and *Plesianthropus* the pattern of the third molar has become modified in the direction of "plus pattern," resembling much more certain molars of primitive man than the same tooth in the anthropoids. In *Pithecanthropus* the third molar is too badly preserved to allow of further discussion.

Summary. On the dentition of the Australopithecinae, Gregory and Hellman (1938) give the following summarizing remarks:

We found that the forms called *Plesianthropus transvaalensis* and *Paranthropus robustus* by Broom displayed in their adult dentitions the following characters which are transitional or intermediate between the ape and human stages: (1) the upper and lower canine teeth, apparently in males as well as females, were of relatively small size, with low tips, and were altogether more human than ape-like; (2) the third upper and lower molars were very large, in contrast to the usually short third molars of man; (3) the second upper molar was larger than the first, as in apes; (4) the third lower molar crown was evidently a derivative of the ancestral five-cusped "*Dryopithecus* pattern," but it was approaching the human "plus pattern" in the arrangement of its grooves and bore a large sixth cusp as in certain primitive men; (5) the grinding teeth when well worn acquired nearly flat occlusal surfaces as in man, whereas in apes the buccal cusps of the upper, and the lingual cusps on the lower, tooth rows, tend to remain in high relief even in well-worn specimens; (6) in the upper dental arch of *Plesianthropus*, as carefully reconstructed by us, the sides were slightly divergent posteriorly and the general effect was more human than ape-like; (7) in correlation with the small size and low crown of the upper canine, the first lower premolar had a convex buccal face and showed little or no trace of the shearing mesiobuccal face which is found in the ancestral *Dryopithecus* stock, where it sheared against the distolingual face of the tusk-like upper canine. Thus the first lower premolars in *Paranthropus* were almost human in stage.

The permanent dentition of *Pithecanthropus* differs from that of the other hominids but approaches that of the Australopithecinae in the following peculiarities: (1) The first upper premolar has three roots. (2) The second upper molar is larger than the first. (3) The second lower premolar is very large, surpassing in its absolute as well as its relative length (in comparison with the first molar) the same tooth in recent man. (4) There is a decided increase in length from the first to the third lower molar, the latter being the largest tooth of the whole series.

If we compare this statement with that of Gregory and Hellman quoted above, we find that neither the relation in size between the second and the first upper molars nor the increase in length of the lower molars any longer constitutes a difference between the Australopithecinae and Hominidae. The similarity of the lower dentition, the intermediate stage being represented by *Pithecanthropus*, is shown in table 4, page 217.

Deciduous Dentition

The deciduous dentition of *Australopithecus*, according to W. Abel, shows signs of higher specialization than the same dentition in recent man. This may be true--we know too little about the deciduous dentition of fossil Hominidae to follow the line of evolution--but it is no reason for denying, as Abel does, any closer relationship between *Australopithecus* and *Homo*. There are other reasons, to be discussed below, why *Australopithecus* cannot be ancestral to man but must not, however, be excluded from the human family.

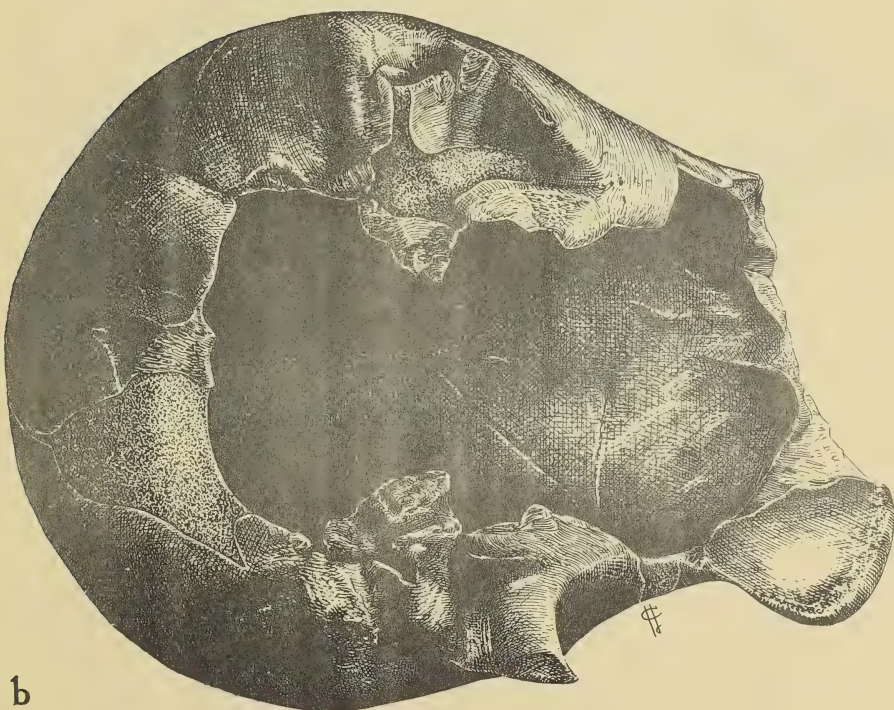
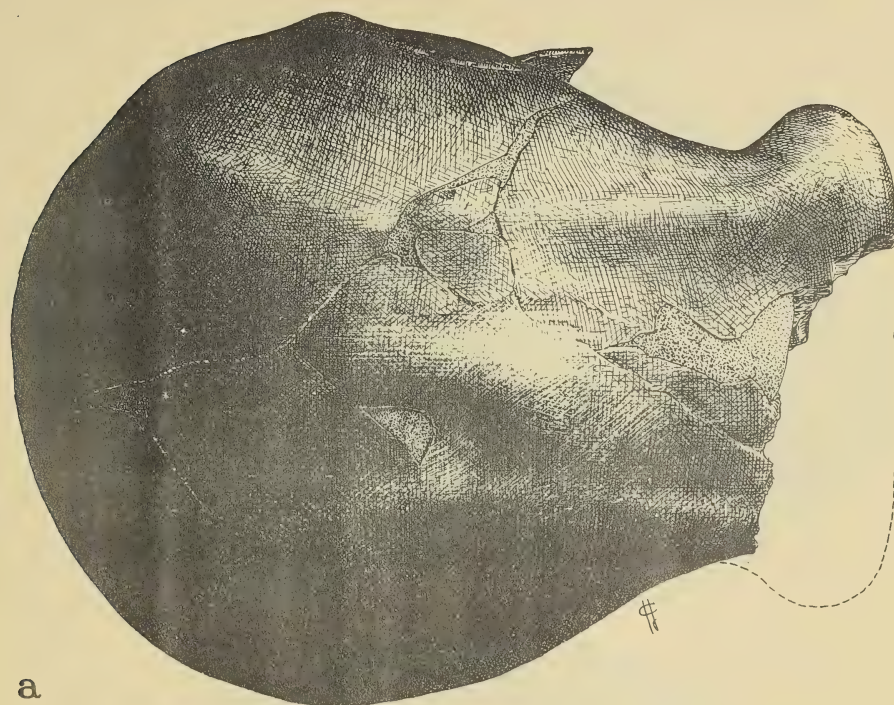


Fig. 1. *Pithecanthropus* II. a, norma horizontalis; b, norma basalis. $\times 0.65$.

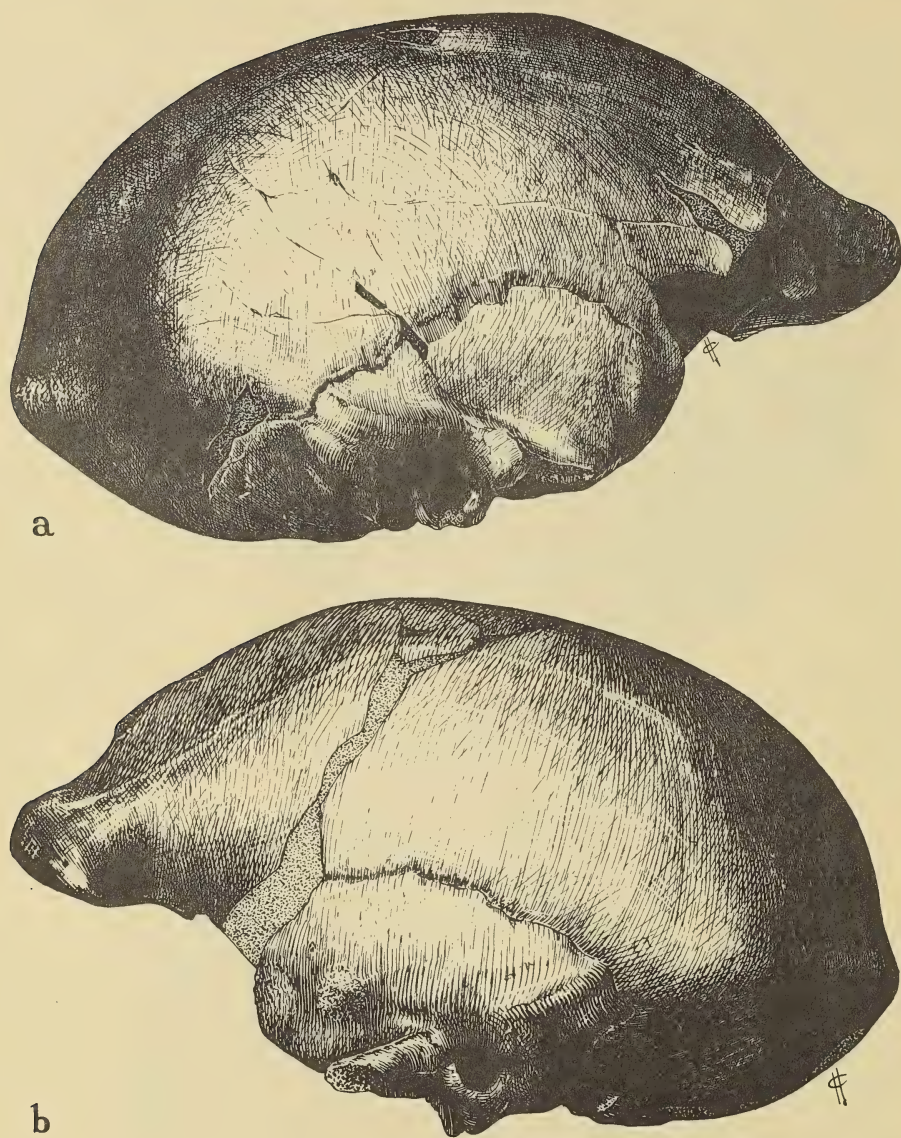


Fig. 2. *Pithecanthropus* II. Norma lateralis: a, right side; b, left side. $\times 0.65$.

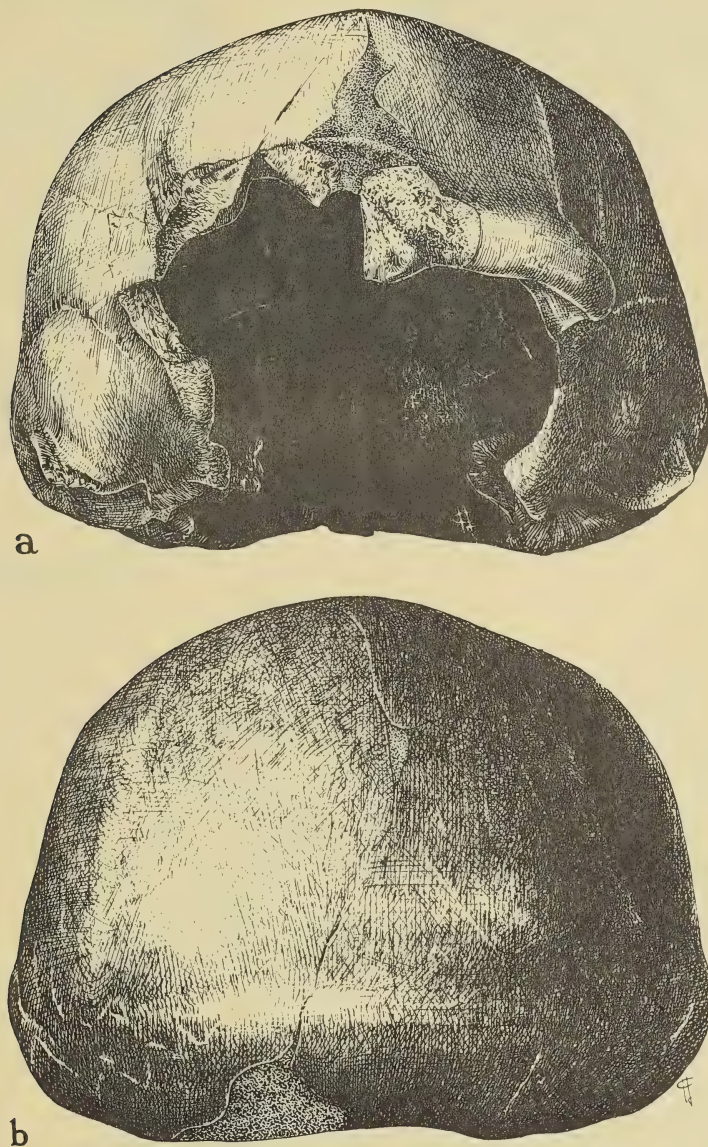
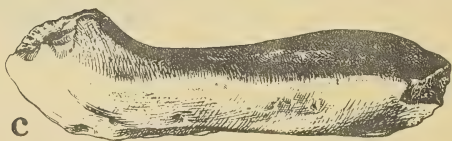
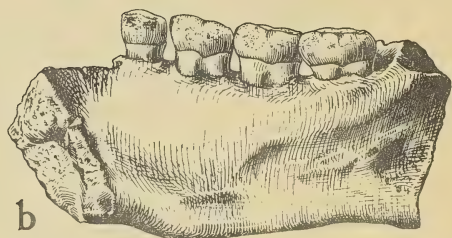
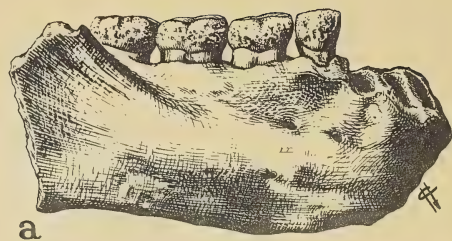
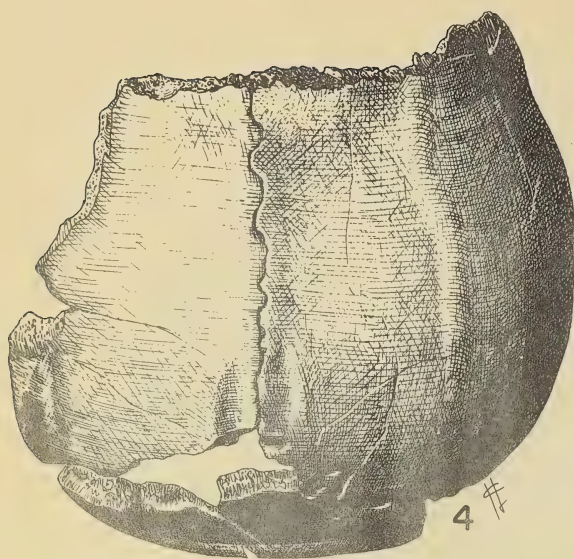
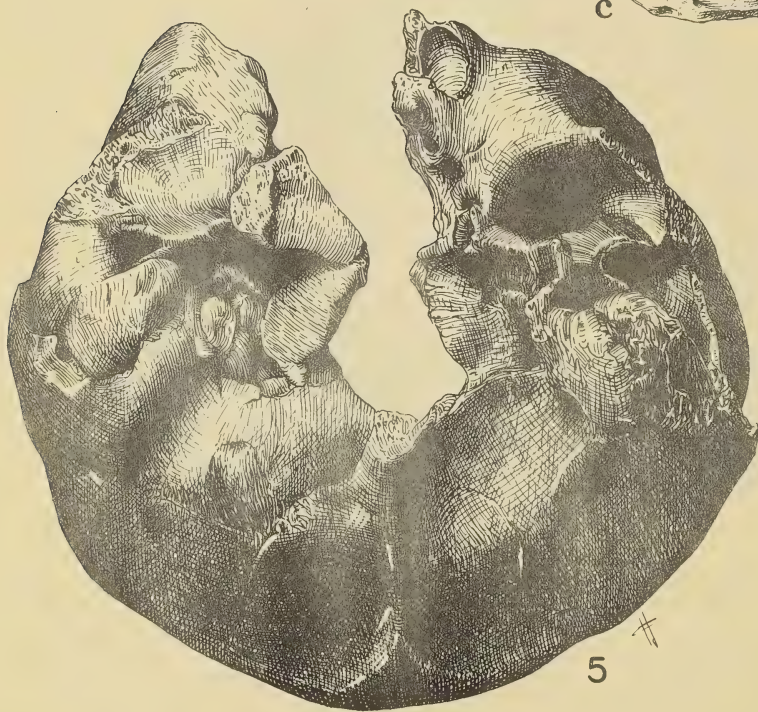


Fig. 3. *Pithecanthropus* II. *a*, norma frontalis; *b*, norma occipitalis. $\times 0.65$.



6



5

Fig. 4. *Pithecanthropus* III. Norma horizontalis. $\times 0.65$.

Fig. 5. *Pithecanthropus* IV. Norma basalis. $\times 0.65$.

Fig. 6. *Pithecanthropus* B. Fragment of lower jaw, right side: a, lateral view; b, medial view; c, basal view. $\times 0.65$.

TABLE 4

Comparison of lower dentition

	Anthropoid apes	<i>Paranthropus</i> <i>Plesianthropus</i>	<i>Pithecanthropus</i>	<i>Sinanthropus</i>	<i>Homo</i> (recent)
Canine (C)	Large	Small	Small	Small	Small
First premolar (P ₃)	Uni- or bicuspid "Sectorial" Large	Bicuspid Nonsectorial Large	Not known	Bicuspid Nonsectorial Large	Bicuspid Nonsectorial Small
Second premolar (P ₄)	Bicuspid Large	Bicuspid Large	Bicuspid Large	Bicuspid Large	Bicuspid Small
First molar (M ₁)	Pentacuspid	Pentacuspid	Pentacuspid	Pentacuspid	Pentacuspid
Second molar (M ₂)	Pentacuspid Larger than M ₁	Pentacuspid Larger than M ₁	Pentacuspid Larger than M ₁	Pentacuspid Same size as M ₁	Quadricuspid Smaller than M ₁
Third molar (M ₃)	Pentacuspid Larger than M ₂	Penta- or hexacuspid Larger than M ₂	Penta- or hexacuspid Larger than M ₂	Pentacuspid Reduced	Irregular Reduced
Mandibular arch (M ₃ -P ₄)	Straight or slightly concave	Slightly convex	Slightly convex	Slightly convex	Slightly convex

The writer cannot follow Abel, who suggests relations to gorilla. The first lower deciduous molar of the Taungs skull (of which the drawing given by Gregory, 1934, fig. 71, gives a much better idea than the photographs of the cast published by Abel), with the broad mesial end and the protoconid and metaconid well separated, can be compared only with the same tooth of man. In the anthropoids this tooth shows a very dominant protoconid; it is more or less unicuspid in gorilla or with a very weak and unimportant metaconid in orang and chimpanzee, foreshadowing more or less in its general appearance the "sectorial" premolar which takes its place in the permanent dentition.

RELATIONSHIP BETWEEN AUSTRALOPITHECINAE AND MAN

We have seen that in the permanent as well as in the deciduous dentition of the Australopithecinae there is no characteristic to force the exclusion of this group from the Hominidae, using the word in a broad sense.

But when we try to point out the relationship to *Homo*, we must state that the Australopithecinae cannot be ancestral to man. There are two main reasons: they are geologically too young (the group is of Pleistocene age only), and their teeth are too large.

This latter reason needs some explanation. It is a general law that small forms prevail at the beginning, and large at the end of an evolutionary line. The Cretaceous mammals were only as big as rats; the earliest forerunners of the horse had the size of rabbits, those of the elephants, that of tapirs. The anthropoid apes from the lower Tertiary of Egypt are smaller than the living gibbons, and *Tarsius*, the most primitive of the existing primates, is at the same time the smallest.

For man, too, we must assume small ancestors which became larger in the course of evolution. This increase finds its clearest expression in the development of the brain, which, at the same time, marks the evolution of human intelligence. The largest brain capacity observed among the living anthropoids is about 650 cc. for a male gorilla. In *Pithecanthropus*, our most primitive ancestor, we have evidence that the capacity is only 800-1000 cc.; in *Sinanthropus*, the Peking man, 900-1200 cc. In Neanderthal man the capacity is already about 1250-1400 cc. (for the big skull of La Chapelle even 1620 cc.), and in recent man of the white race it is 1350 cc. (female, average) and 1500 cc. (male, average). There are also signs of an increase in body size. Weidenreich estimates the height of a female *Sinanthropus* at only 152 cm., that of Neanderthal man at 155-160 cm.

At the same time, however, a reduction of the jaws and of the dentition is observed. Neanderthal man has larger teeth than recent man, but the teeth of Peking man are still larger, and the largest teeth are found in *Pithecanthropus* (see table 5). This reduction of the teeth and simultaneous rapid development of the brain must have been caused by something we do not

find in the animals. In recent man we find the primitive Negroes and Australian aborigines macrodont, with strong and beautiful teeth if they live under natural conditions, but with very bad teeth if they try "civilized" conditions; and the white race microdont with small and bad teeth.

TABLE 5

Length (in millimeters) of the three lower molars

<i>Plesianthropus transvaalensis</i>44.3
<i>Pithecanthropus erectus</i>40.0
<i>Sinanthropus pekinensis</i> (G)37.7
<i>Homo heidelbergensis</i>36.5
<i>Homo neanderthalensis</i> (Krapina G)36.5
<i>Homo sapiens</i> :	
Australians33.1
Whites: males32.0
females30.6

Homo sapiens (average) after Gregory and Hellman (1926).

The influence of civilization on the choice of food and on the dentition is too evident to need detailed discussion here. Moreover, civilization in its earliest stages is very old; we can trace it back to the Lower Pleistocene, back to the Peking man. When the writer had the privilege of visiting the *Sinanthropus* site at Chou-Kou-Tien under the guidance of C. C. Young, he was struck by the numerous artifacts and the large ash layers. There can be no doubt: Peking man did not make implements accidentally, he was already accustomed to their use. The quartz he used to make his implements was a bad material, but he had no other; if he had used flint we should be astonished at the various tools he was able to produce. He even knew how to maintain a fire for long periods, since the ash layers of his fireplaces have, in some cases, a thickness of more than a meter. Bones are often split and sometimes burned (including human bones!), indicating that Peking man even knew how to roast meat. Indeed, the civilization of that primitive forerunner of ours was not so very different from that of the Australian aborigines of today.

The invention of implements and tools and the discovery of the use of fire must have had the deepest influence on the evolution of man. It marked the level which separated him from the animals; it raised him above the anthropoids. The implement in his hand is an inspiration. It is the victory of intelligence over brute force. Now he is no longer an animal among animals, living in the forests and searching for food; he becomes a hunter, can make tools, learns how to build a home, and is able to develop art. And when his food is cooked, he changes completely from an anthropoid to a human diet.

We have to assume in man's earliest forerunners a moderate increase in size both of the prehuman dentition and of the prehuman brain, in about the same degree as we find it in the living anthropoids. After the invention of

implements, however, he no longer needed his teeth to tear his food to pieces, nor big jaw muscles which pressed his braincase. The skull of a young anthropoid is rounded and much more human-like than an adult one, which changes its form under the pressure of enormous jaw muscles. Even in *Pithecanthropus* we observe that the juvenile skull from the Lower Pleistocene of Modjokerto (*Homo modjokertensis*) has a more human appearance than the adult ones. Soon man discovered the use of fire and began to cook his food. He used his teeth in a different way from his anthropomorphic ancestors. When he began to talk he also used his jaw muscles in a different way. Only in the development of civilization can we find a reason for the typically human evolution: the reduction of the dentition combined with an astonishing, progressive development of the brain--the two surely interdependent.

As is shown above, the reduction of the human dentition is a fact we can prove. Man must, therefore, have had a forerunner whose dentition had the maximum size possible in the line of evolution which leads to recent man. There are reasons for believing that this may have been *Pithecanthropus*, since artifacts have been found in the upper level of the *Pithecanthropus* layers in central Java; and if this assumption is correct, then every human-like being having bigger teeth than *Pithecanthropus* must be excluded from the direct line of human evolution.

Since the teeth of *Pithecanthropus* as well as of *Sinanthropus* show a very complicated crown pattern with numerous wrinkles, not so different from the teeth of some anthropoid apes, the teeth of our earliest forerunners may have been unlike the teeth of recent man, which are reduced in both pattern and size and do not show the original primitive pattern, as is suggested by some authors.

The intelligence of the human race varies considerably, from that of highly civilized people in America and Europe to that of primitive hunters without clothes and using stone implements in Australia. Differences in intelligence have certainly prevailed as long as the world has existed. It is highly probable that only a very small and progressive group of our fossil ancestors was able to invent implements, make use of intelligence, and give rise to the earliest civilization. The others were not predestined: they followed the regular way of "animal evolution," showing no reduction of the big jaws and of the dentition and, in consequence, only an insignificant increase of the brain.

Such a group seems to have been preserved in the Australopithecinae from South Africa, far away from Asia, the center of human evolution. They fulfill both suppositions postulated above: they are of Pleistocene age, and thus contemporary with *Pithecanthropus* and *Sinanthropus*, real prehomnids; and the teeth of all three species of them are larger than those of *Pithecanthropus*. All this leads to the conclusion that the Australopithecinae have to be included in the human family (familia Hominidae) and that they represent, not a branch

parallel to the human line, but a real side branch (perhaps connected by a common ancestor of Pliocene age) which demonstrates what man would be like without the divine inspiration, civilization.

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PLATES



All figures $\times 0.35$

- FIG. 1. *Pithecanthropus* I (Dubois, 1891). Norma horizontalis.
FIG. 2. *Pithecanthropus* II (von Koenigswald, 1937). Norma horizontalis.
FIG. 3. *Pithecanthropus* I. Norma basalis.
FIG. 4. *Pithecanthropus* II. Norma basalis.



All figures $\times 0.35$

FIG. 1. *Pithecanthropus* I (Dubois, 1891). *D*, ear opening, as reconstructed by Dubois.

FIG. 2. *Pithecanthropus* II (von Koenigswald, 1937). *e*, ear opening, as observed in skull II.

FIG. 3. *Pithecanthropus* I. Norma occipitalis.

FIG. 4. *Pithecanthropus* II. Norma occipitalis.

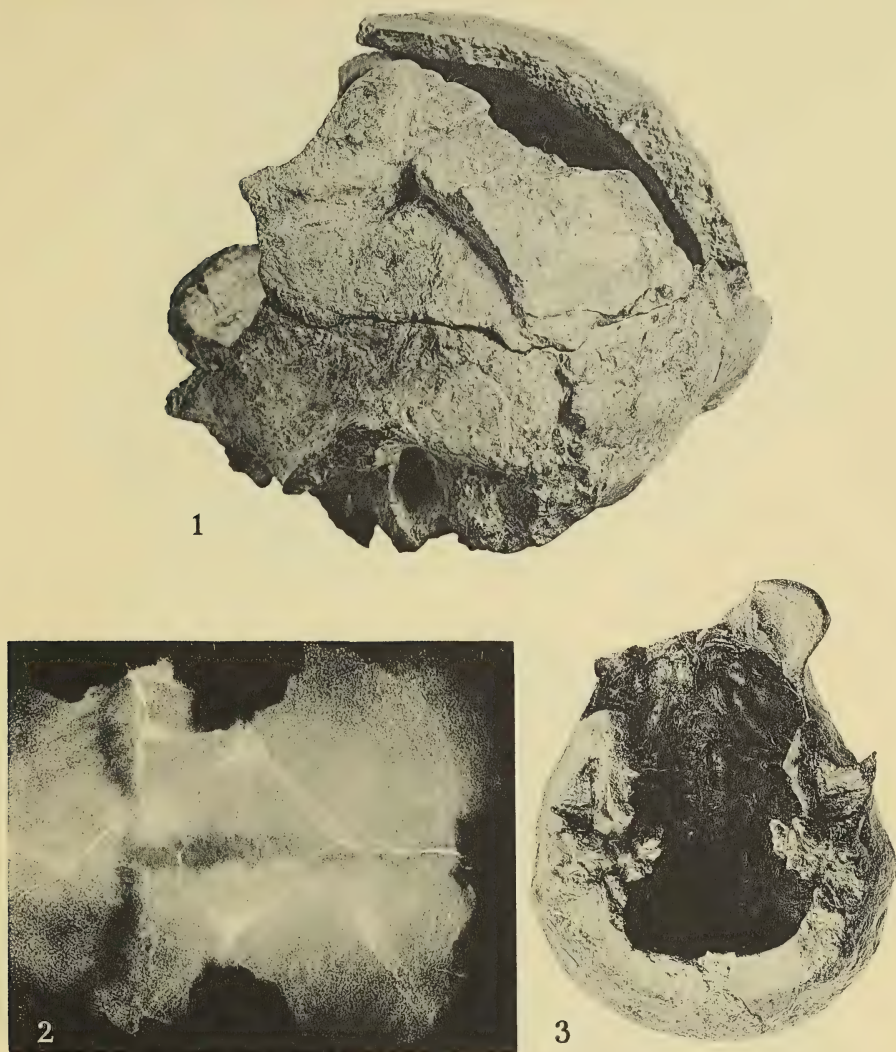
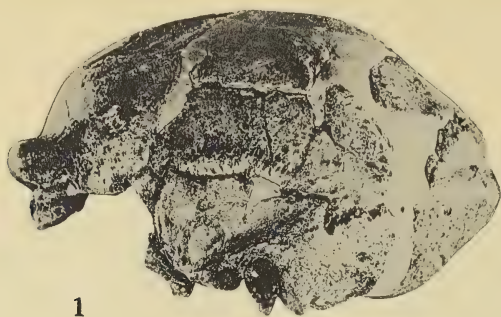


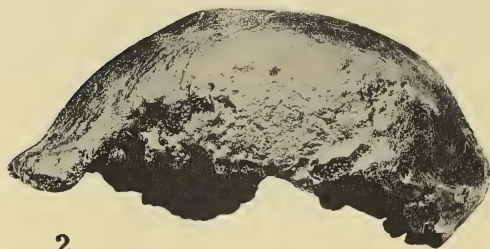
FIG. 1. *Pithecanthropus* IV. Norma lateralis, left side. $\times 0.6$.

FIG. 2. *Pithecanthropus* II. Roentgenogram of the frontal-parietal region, showing sutures (bregma point). $\times 0.6$.

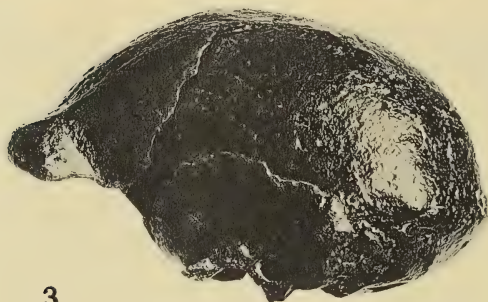
FIG. 3. *Pithecanthropus* II. Norma basalis. $\times 0.33$.



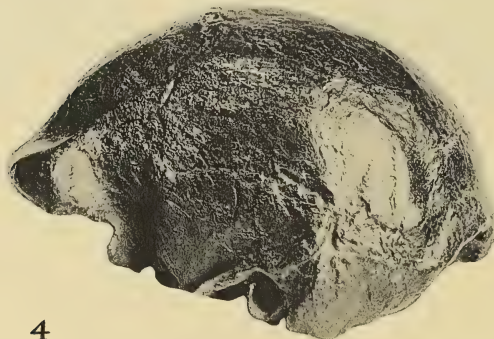
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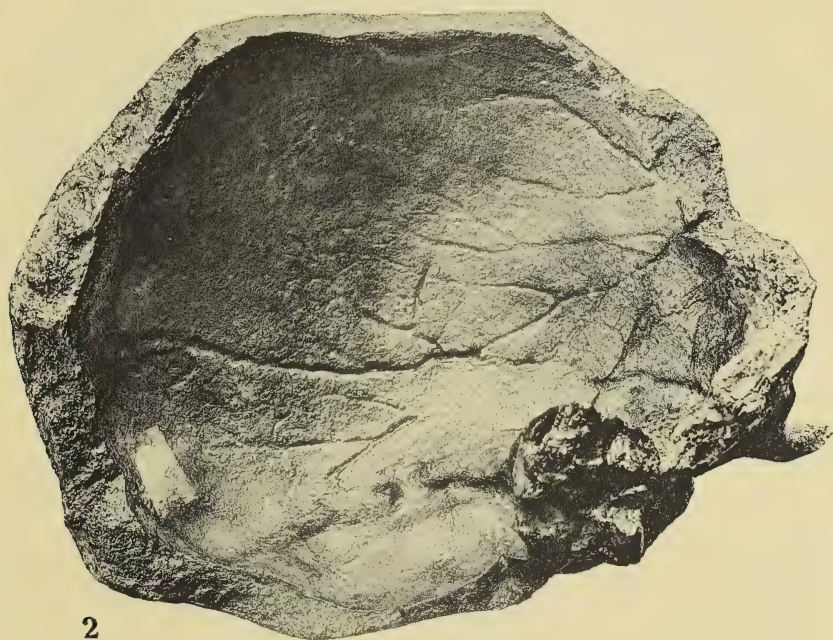
FIG. 1. *Sinanthropus pekinensis* Black, skull II. Lateral left view (Weidenreich). Chou-Kou-Tien, China.

FIG. 2. *Pithecanthropus erectus* Dubois, skull I (Dubois). Trinil, Java.

FIG. 3. *Pithecanthropus erectus* Dubois, skull II (von Koenigswald). Sangiran, Java.

FIG. 4. *Homo (neanderthalensis) soloensis* Oppenoorth, skull XI (Geol. Surv. N. E. I.). Ngandong, Java.

Photographs by Peking Union Medical College, Peiping



Pithecanthropus II. $\times 0.8$

FIG. 1. Fragment of left side of skull, with ear opening

FIG. 2. Same skull fragment, inner view, temporal region



Pithecanthropus IV. $\times 0.35$

FIG. 1. The fragments before cleaning

FIG. 2. The fragments after cleaning

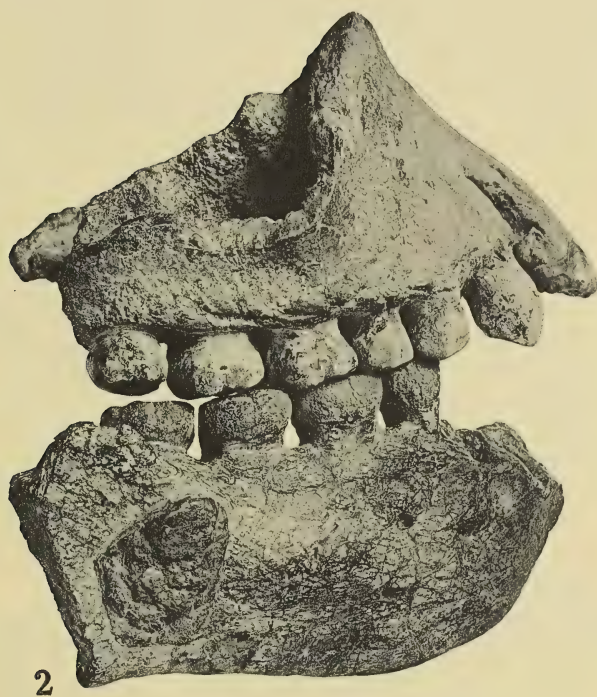
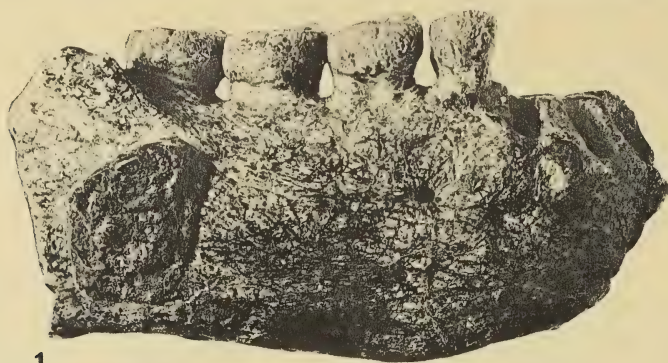


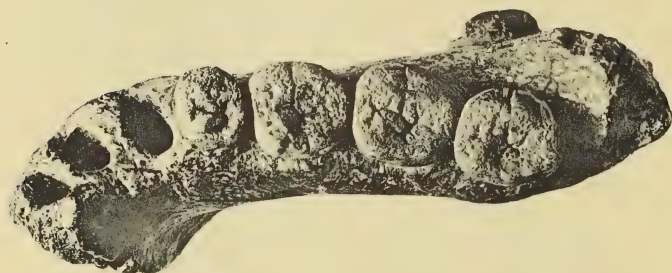
FIG. 1. *Pithecanthropus* III. Norma frontalis. \times approx. $\frac{2}{3}$.
 FIG. 2. *Pithecanthropus*. Upper jaw from IV, lower jaw from B. \times 0.9.



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2



3



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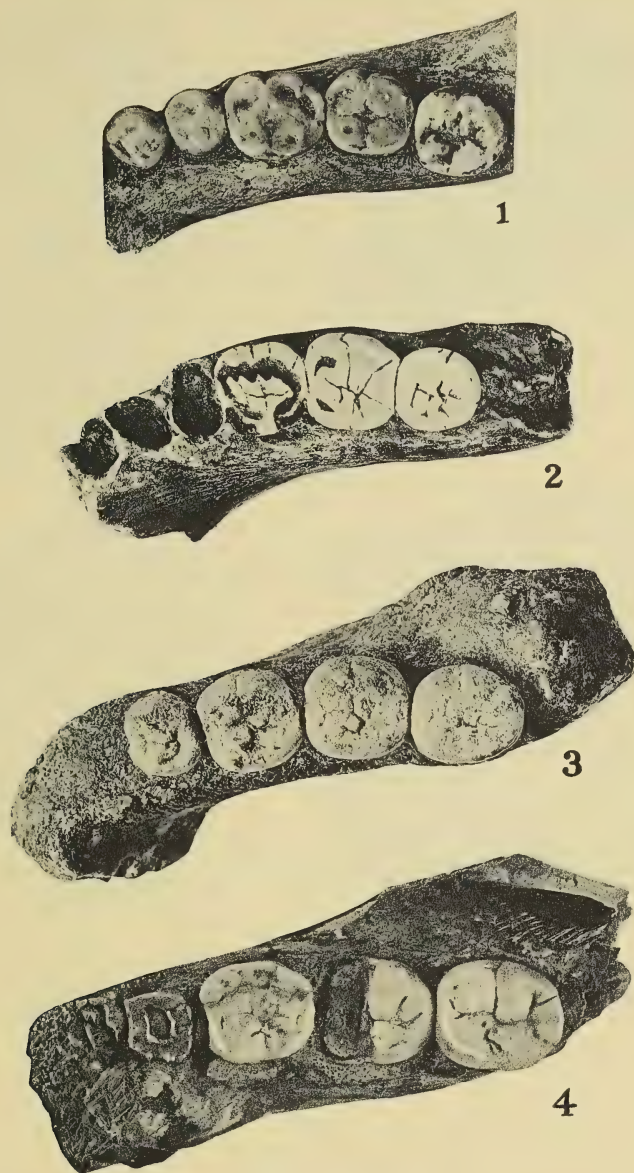
Pithecanthropus B. Fragment of lower jaw, right side. Natural size.

FIG. 1. Lateral view

FIG. 3. Occlusal view

FIG. 2. Medial view

FIG. 4. Basal view



All figures natural size

FIG. 1. *Homo sapiens* Linné. Right lower jaw (with molars and premolars) of a male individual. Prehistoric, Java.

FIG. 2. *Sinanthropus pekinensis* Black. Right lower jaw AII (with the three molars) of a female individual. Lower Pleistocene, Chou-Kou-Tien, near Peiping, China. (From a cast.)

FIG. 3. *Pithecanthropus erectus* Dubois. Right lower jaw B (with three molars and second premolar) of a male individual. Lower Pleistocene, Sangiran, central Java.

FIG. 4. *Paranthropus robustus* Broom. Right lower jaw (with the three molars) of a male individual. Middle Pleistocene, Kromdraai, Transvaal, South Africa. (After Broom.)



Pithecanthropus IV. Reconstruction by F. Weidenreich and O. Falckenbach. $\times 0.3$.

Photographs by American Museum of Natural History, New York

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